THE UNIVERSITY OF ALBERTA

SPATIAL AND TEMPORAL UTILIZATION OF SEMI-NATURAL ENCLOSURES BY

CLETHRIONOMYS GAPPERI, CLETHRIONOMYS RUTILUS

AND *PEROMYSCUS MANICULATUS*

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Spatial and temporal utilization of semi-natural enclosures by *Clethrionomys gapperi*, *Clethrionomys rutilus* and *Peromyscus maniculatus*" submitted by Jack Friesen, in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Clethrionomys gapperi, *C. rutilis* and *Peromyscus maniculatus* were maintained in outdoor enclosures at Heart Lake, Northwest Territories, and Lacombe, Alberta, for varying lengths of time. Activity was measured with door-operated switches on nest boxes and feeders connected to an event recorder.

Snow depth, hours of light, air and subnivean temperatures, relative humidity and wind were recorded and related to changes in animal distribution at different population densities in an artificial habitat gradient.

Tests between *C. gapperi* and *C. rutilus* that had access to each other's area in enclosures were used in conjunction with behavior tests to try to discover some cause for the sharp demarcation of these contiguously allopatric species. A test between the sympatric species *C. gapperi* and *P. maniculatus* was conducted for comparison.

C. gapperi had a 2 to 5 hr activity cycle throughout the year. *C. rutilus* had the same cycle during the time it was tested (summer). *P. maniculatus* was nocturnal with occasional arhythmic daytime activity. Activity peaks were synchronized mostly with sunrise but sometimes also with sunset. Frequency of peaks for *C. gapperi* increased slightly in summer during the reproductive season. Activity also tended to be more intense during the day in winter and during the night in summer.

Daily activity level was affected by extremes in relative humidity in summer and by air temperature in winter. Activity was highest during summer when animals were agonistic and lowest during

winter when numbers were lowest and animals were gregarious.

Each of the three species tested showed a preference for one pen over others. The "good" habitat was used to rear litters in summer and for nesting in winter. Juveniles were forced to move to less favorable habitat shortly after weaning and showed a greater summer mortality than adults.

C. gapperi and *P. maniculatus* simultaneously raised litters in the same pen. *C. gapperi* and *C. rutilus* did not share the same pen when one or both were pregnant or lactating. Intraspecific aggression prevented two females of the same species from sharing a pen while litters were being raised. *C. gapperi* were more successful in raising litters than *C. rutilus*.

Intraspecific aggression seemed to be higher than interspecific aggression. *C. gapperi* were most aggressive and showed the highest exploratory tendencies based on open field tests.

It is proposed that *C. gapperi* and *C. rutilus* are at present separated along the Kakisa River by competitive exclusion due to behavior which may be mainly mutual avoidance.

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INTRODUCTION

The present study was undertaken to investigate some aspects of the activity and behavior of *Clethrionomys gapperi, C. rutilus* and *Peromyscus maniculatus* in outdoor enclosures.

The following hypotheses were tested: (1) that timing and amplitude of circadian rhythm correlate with some or all of sunlight, temperature, relative humidity, wind speed and snow depth; (2) that the small rodents used in this study alter their behavior from summer to winter to conserve energy and reduce mortality during the time when competition would not benefit the species; (3) that animals in a diverse habitat use the most suitable part first moving to the least suitable when population pressure increases, and that a dominance hierarchy forms with adult males at the top, followed by adult females with juveniles at the bottom; (4) that the similar species *C. gapperi* and *C. rutilus*, which are allopatric in nature, would not tolerate one another in the same pen and that neither species would be able to displace the other from an established area; (5) that the dissimilar species *C. gapperi* and *P. maniculatus*, which are sympatric in nature, would share the same habitat.

Small rodents have often been used in enclosures for population studies (Bailey 1966, Getz 1969, Grant 1969, Fisler 1970), because they are easily captured, readily maintained and because they have short life cycles. Populations usually build quickly by natural increase and then can be manipulated to respond to various experimental conditions. One

additional important reason for using enclosures is the fact that behavior of small microtines can rarely be observed in the wild. Even winter tracking is difficult. Formozov (1946) found that when animals were readily caught by placing traps under the snow they rarely showed up on the surface even under good conditions.

Since many voles are known to build winter nests on the soil surface even though their summer nests are subterranean (Formozov 1946) the test apparatus was a compromise to provide a maximum of opportunity to measure and observe activity while subjecting animals to conditions as near normal as possible. Nest boxes on the soil surface within the enclosures provided animals with a nest which approached subterranean nests in darkness and protection from weather in summer and took advantage of the insulating properties of snow and flow of heat from the soil in winter.

Many methods and devices to study the activity and movement of small mammals in the wild and in pens have been reported. Crowcroft (1959) used a simple method whereby he manually recorded direct observations on a series of mimeographed diagrams of his test pen. Pearson (1960), at the other extreme, recorded the passage of animals with an elaborate apparatus including an automatic camera that was activated by a photoelectric cell in a natural runway. Kavanau (1963) did a complex multifactor analysis but his apparatus was very small and unnatural. Other less complex methods include: analysis of fecal pellets of a predator (Spitz and St. Girons 1969), dye excretion of small mammals (Brown and Conaway 1961), a suspended cage connected to a kymograph (Healey 1967), swinging doors with electrical switches (Gorecki

and Hanusz 1968, Stebbins 1971), and radio-isotopes affixed to animals

(Karulin 1970). Several of the above methods were used in the present

study but the major emphasis was on the use of nest boxes and feeders

monitored with swinging doors and mercury switches like those of

Stebbins (1971).

The first aspect of the study concerns daily fluctuations of

activity. Circadian rhythms (approximately 24 hr cycles) have been the

object of numerous investigations (Davis 1933, Pearson 1957, Pearson

1962, Toderovic 1966, Goff and Finger 1966, Stebbins 1970). However,

most of the above tests were conducted with one or two animals at a

time eliminating the possibility of activity fluctuations due to chang-

ing interactions between animals.

I attempted to correlate activity of grouped animals to

quantitative and broadly qualitative environmental changes because

weather may affect activity directly and indirectly by altering the type

of behavior of the animals.

The second part of this study compared the breeding and non-

breeding seasons. *A priori* it might be expected that small mammals

would have to decrease their activity during protracted periods of cold

to conserve energy and it has been known for some time that some voles

are active throughout the year (Hatt 1930, Formozov 1946). Small

animals can keep active during winter because of snow cover. At a

depth of 20 to 25 cm the protective effect of snow smooths the

fluctuations of the subnivean temperature (Formozov 1946) which hovers

between 15° and 20° F with only slow changes (Pruitt 1965). Winter

breeding is possible under such conditions and has been reported in

lemmings for example (Fuller 1967). However, winter breeding has not

been found to occur in the species used in this study (Fuller *et al.*

1969). It would seem that a reduction in the usual summer aggression

(Watts 1970) shown by *Clethrionomys* would increase winter survival by

confining activity to feeding and reducing injuries from fighting,

especially to smaller animals. A return to aggressive behavior in spring

would again provide a mechanism to disperse animals and perhaps play a

part in population control discussed in the following section.

The third aspect of this study was based on the assumption that not

all parts of a habitat available to a species are equally suitable and,

therefore, only the best parts would be used during low population levels,

while marginal areas would be used during high levels of population.

Competition is assumed to be keener with increasing density resulting in

subordinate animals being forced to move to marginal areas.

It has been reported that some small mammals aggregate during

winter (Formozov 1946, Beer 1961), perhaps to conserve heat, or perhaps

to use the best parts of a mosaic of good and bad habitats (Fuller 1967).

There are, then, at least two possible reasons for a seasonal change in

density of animals in any particular area. Intraspecific aggression may

cause a lower density in the best habitat in summer which favors raising

of litters and a relaxation of aggression (competition) in the same

areas in winter to allow a higher density and thus a greater number of

survivors for breeding the following spring.

Van Vleck (1968), Stickel (1946), and Webb (1965) found movements

of small mammals readily took place from areas of high density to

trapped-out areas. Getz (1970) found *Microtus* occupying only wet areas

during a population low with movement to drier areas when numbers

increased. Lidicker (1962) postulated a genetic selection for emigration

tendency during population peaks. Christian and Davis (1964) reported

an endocrine feedback system which caused the level of intraspecific

aggression to fluctuate. Sadleir (1965) and Healey (1967) postulated

that aggression increased during the breeding season but that it was

directed towards newcomers from outside the immediate family area. Krebs

(1970) suggested that intraspecific agonistic behavior causes dispersal

movements which can be a critical factor in regulating the density of

small mammal populations.

This study attempts to describe the distribution of a few species

under controlled conditions and suggests some reasons for the observed

phenomena.

The fourth hypothesis stems from the unusual distribution of

three species of small rodents in the area of this study. *P. maniculatus*

is sympatric with both *C. gapperi* and *C. rutilus*. However, there is a

sharp boundary between the North American species *C. gapperi* and *C.*

rutilus of northwestern North America and northern Eurasia with no known

overlap in range (Hall and Kelson 1959). That boundary follows the

Kakisa River in the study area (Fig. 1). Some aspects of the ecology of

these species previously studied in this area are: weather (Fuller,

Stebbins and Dyke 1969), food habits (Dyke 1971), reproduction and

synchrony of cycles (Fuller 1969), serum protein variation during cycle

changes (Canham and Cameron 1972) and behavioral interactions (Murie

1972).

Difficulties have been encountered in trapping animals close to

the boundary along the Kakisa River. It is possible that asynchrony of cycles of *C. rutilus* at Fort Providence and *C. gapperi* from Heart Lake would not necessarily indicate asynchrony right at the Kakisa River. Similarly the use of animals trapped approximately 60 km on either side of the Kakisa River in the present study may not reflect the interactions of animals living at the boundary of their ranges. Nonetheless, animals of the species *C. gapperi* and *C. rutilus* were allowed to interact under conditions that allowed measurement of activity levels, reproductive success and observations of behavior. Studies of interspecific interactions were conducted only during spring and summer on the premise that dispersion in the wild occurs only at those times and therefore that interspecific interactions were not likely to occur in the winter. This also assumes that the small mammals studied would be least likely to cross the Kakisa River in the winter when it would seem easiest for them to do so.

Gause (1934) contended that whenever two species with closely overlapping requirements are confined to a limited space, one species will eventually die out. This has become the principle of competitive exclusion and has received considerable attention over the years. Birch (1953) supported the theory, while Andrewartha (1961) stated that the theory was not relevant because no two species are likely to have identical requirements nor is intense crowding a problem in nature. Ayala (1972) stated that the theory was not universally true and showed that two or more closely related species of *Drosophila* competing for the same resources could coexist for long periods under certain conditions.

Competitive exclusion of one species of *Microtus* by another closely related species was demonstrated by Findlay (1954), Koplin and Hoffman (1968) and Murie (1971), where one species was restricted to xeric habitats and the other to hydroseres where they were sympatric. Where they were allopatric each vole occupied both types of habitat. When habitat segregation occurred it was thought to be due to mutual avoidance behavior. Murie (1969) also showed substrate selection to be a factor contributing to segregation of the two species.

A number of studies showing competitive exclusion between the genera *Microtus* and *Clethrionomys* have been conducted in enclosures (Grant 1969), in aspen parkland by live trapping (Morris 1969), and by comparison of faunas of offshore islands adjacent to North America (Cameron 1965) and Great Britain (Corbet 1961). In these studies segregation again occurred at the edge of two habitats, forest and meadow, or at a natural barrier that was difficult to cross. Grant (1969) and Corbet (1961) found that *Microtus* excluded *Clethrionomys* from grassland. Morris (1969) found that *Clethrionomys* excluded *Microtus* from the aspen habitat, contrary to the results of Kucera and Fuller (unpubl.). Cameron (1965) and Grant (1970) concluded that whichever genus reached an island first established a "beachhead" that prevented the other from becoming established.

The boundary between *C. gapperi* and *C. rutilus* at the Kakisa River seems similar to the above situations though there are some important differences. First the two species of *Clethrionomys* have nearly identical (as far as can be determined) requirements regarding food and nesting sites (Dyke 1971). Secondly the habitats appear to be

the same on both sides of the river. Finally the Kakisa River probably
acts as a partial barrier or filter (compatible with the filter concept
suggested by Simpson (1953) in zoogeography) but it would not seem too
difficult to cross especially since *C. rutilus* has already crossed the
much wider Mackenzie River. Since 1961 four *C. rutilus* have been caught
southeast of the river while no *C. gapperi* have been caught to the
northeast, and though the possibility exists, no hybridization along
the boundary has been found (Fuller 1969). It might also be noted that
the boundary between the two species of *Clethrionomys* seems fairly sharp
along the Alaska Highway where there is no noticeable barrier (Rand
1944).

It is possible that subtle behavioral differences between *C.*
gapperi and *C. rutilus* are keeping them separated. Two traits that
would seem important to a species for successful occupation of an area
or movement into new areas are aggressive and exploratory tendencies.
Since these are difficult to test in the field, laboratory tests were
used. An open field test commonly used in psychology and zoology
(Fredericson 1953, Broadhurst 1957, Henderson 1967, Krebs 1970) was
employed as an indicator of exploratory behavior. Aggressive behavior
was tested in an arena similar to those used by King (1957), Getz (1962)
and Krebs (1970).

The fourth area of this study reflects the view that *C. gapperi*
and *C. rutilus* probably met at or near the present boundary of their
ranges during post glacial times (Macpherson 1965) and that they are
presently at a standoff. The two species may be too similar in habits
to occupy the same range at the same time yet neither species is

aggressive enough to displace the other during periods when they are dispersing and most likely to be expanding their ranges. This would be the case if juveniles were the dispersing individuals.

The present study attempted to increase the population pressure and consequently the need to disperse in order to determine if one species could displace the other. Greater opportunity was also provided for interbreeding due to increased possibility of contact between species.

MATERIALS AND METHODS

ACTIVITY ENCLOSURES

Activity tests were carried out at the Heart Lake Biological Station in the Northwest Territories and at Lacombe, Alberta. The former is located at 60° 51' N, 116° 37' W, while the latter is located at 52° 28' N, 113° 45' W (Fig. 1).

Heart Lake 1970

The first enclosure was constructed in July 1970 at Heart Lake adjacent to the laboratory (Fig. 2). The enclosure had overall dimensions of 4.8 by 7.2 m subdivided into six pens each 2.4 m square. It contained two units of three pens arranged in a line set side by side (Fig. 3). The walls were sheets of 24 gauge galvanized steel 60 cm high held together with sheet metal screws. Wood strips 5 by 10 cm were affixed to the upper edges of the sides to provide extra rigidity and to cover the wiring connecting the switches within the enclosure to the event recorder. A narrow strip of topsoil was removed beneath the walls and replaced with a ribbon of concrete to join the sheet metal to bedrock which was located 15 to 20 cm below the surface. Ports were provided to allow animals to move freely from one pen to another within a unit. A port was added in 1971 to allow passage between units via pens B and E (Fig. 3).

One feeder (Fig. 4) containing Rockland Mouse/Rat Diet and sunflower seeds was provided in each unit. Food could be added to the

feeder during winter without disturbing subnivean tunnels.

Each nest box, feeder and port between pens was fitted with a short passageway containing a swinging door, which was in turn attached to a Honeywell mercury switch (Fig. 5). Movement of an animal through the passageway completed a circuit to record the event on a 20-channel Esterline Angus event recorder (Fig. 6).

A habitat gradient was established in each unit in the following manner. The pens with "good habitat" (A and D) contained four large (20 by 30 by 16 cm high) nest boxes. Each nest box had two compartments, one of which was insulated on all surfaces with 2.5 cm of styrofoam. This pen also contained a feeder with attached water bottle, four sections of wooden tunnels each 60 cm long, a coniferous tree of approximately 15 cm diameter, and a mixture of low shrubs and grass. The pens with "intermediate habitat" (B and E) had four smaller nest boxes (14 by 14 by 12 cm high) and some low shrubs but lacked feeder, tree and tunnels. The nest boxes had only one compartment and were without insulation. The pens with "poor habitat" (C and F) had only four small (10 by 10 by 8 cm high) uninsulated nest boxes, lacking grass, shrubs, feeder and tunnels.

The first test included continuous monitoring of activity from 1 August 1970 to 31 May 1971. During that time two nest boxes in each pen were connected to the event recorder at any one time, with each pair of nest boxes being monitored for a week at a time.

During late July 1970, caged individuals of both sexes of *C. gapperi* were gradually introduced into the "intermediate" pen of each unit. Animals were released in the pens after varying lengths of time

in cages (1 to 8 days) by placing the cages in the pens and allowing the animals to find their own way out. Twelve animals of various weights (three males and nine females) were put into each unit.

Visual observations of marked animals were made to determine if all individuals were using all pens and nest boxes equally. Several methods of marking animals were investigated and the best was found to be a small, colored, plastic disk attached to the animal's ear by an ear tag. These could be readily distinguished at a distance of 5 to 7 m where the observer's presence did not noticeably disturb the animals.

To determine where the animals spent their resting periods regular censuses were taken when the chart recorder indicated a period of inactivity. These were first taken at 4 to 6 hr intervals then later reduced to two or three a day.

Monitoring the movements of animals over a shorter time span was accomplished using Tantalum 182 and a survey meter. A small amount of Tantalum 182 was glued onto the ear tag of one animal at one time (in each unit). The pens were then monitored every 15 min with the survey meter for approximately 34 hr out of a 48 hr period. Eight of twelve animals in each unit were tested in this fashion.

Lacombe

Another activity enclosure was constructed at Lacombe in September 1970. This was similar to the one at Heart Lake but was only a single unit consisting of three adjacent pens each 2.4 m square. The bottom of this unit was covered with 6 mm hardware cloth to prevent animals from burrowing out. The pens were set on short cropped grass which readily grew through the hardware cloth to provide extra cover.

The unit was situated 14 m from the nearest building between several large, ornamental trees (*Acer negundo* and *Sorbus decora*). Screen tops with a 2.5 cm mesh were placed over the pens to exclude cats (*Felis domestica*).

A habitat gradient was again established using nest boxes of differing sizes and complexity similar to the first enclosure at Heart Lake. The pen with "good habitat" (A) had four tunnels 60 cm long and four nest boxes each containing two compartments one of which was insulated with 2.5 cm of styrofoam. There were no shrubs or trees in any of the pens. However, a feeder with attached water bottle was placed in each pen to determine whether it was the major factor in establishing the gradient.

At the end of September 1970 six *C. gapperi* (three males and three females) from Heart Lake were released in the "intermediate" pen. Each animal was bled from the infraorbital sinus (for associated studies of serum protein phenotyping), toe-clipped and marked with a colored ear tag prior to release. This test was run continuously until the end of May 1972 with subsequent marking and bleeding of all animals born in the pens. Activity was again monitored with an event recorder as at Heart Lake. At Lacombe each nest box and feeder was monitored continuously rather than intermittently. In addition each pen had two nest boxes equipped with thermistors attached to a YSI telethermometer to determine if winter temperatures of the nest boxes differed from each other or from the subnivean temperature.

Heart Lake 1971

A second enclosure was constructed at Heart Lake in May 1971

approximately 50 m from the laboratory in a natural clearing (Fig. 2). This enclosure had overall dimensions and arrangement similar to the first one built there. Construction was also similar except that no trees were within the pens and 6 mm hardware cloth covered the bottom of the enclosure. Activity was monitored as described for the first Heart Lake enclosure. A port was provided to allow animals to move between the two units of the enclosure. This port could be left open and monitored or kept closed. A new system of wiring using diodes (Fig. 7) was devised to allow all nest boxes to be continuously monitored. The first Heart Lake pen was converted to this system in June 1971.

From June to August 1971 tests were conducted in both first and second Heart Lake enclosures to determine what interspecific inter- actions occurred between *C. gapperi* and *C. rutilus*, and also between *C. gapperi* and *P. maniculatus*. In each test two males and two females of one species were placed in the "intermediate" pen of one unit with two males and two females of another species in the "intermediate" pen of the other unit. After approximately a week in which the animals could settle down, the port separating the two species was opened. Changes in activity levels of the two units were noted and a census of nest boxes was taken once or twice a day to determine if one species displaced the other. During those tests observations were made for about a week (before the two units were joined) to determine what intra- specific interactions were occurring. The two species were then allowed to interact for 2 to 3 weeks after which all animals were killed and autopsied to determine their reproductive condition. The hide was removed and examined to detect holes left by bites from other animals.

BEHAVIOR TESTS

In 1971, 112 animals of all three species were tested to measure their tendency to explore new surroundings and 63 males were tested to determine which were dominant over others.

Open Field Tests

All animals trapped in 1971 were given an open field test in an arena 30 by 60 by 30 cm high. The floor of the arena was marked off in a grid of 10 by 10 cm squares. A small holding box (10 by 10 by 10 cm) was attached to one end of the arena (Fig. 8). The arena was lighted by a 60 w bulb 1.5 m above the arena. Observations were made through a small hole in a screen above the arena. An open field test was conducted by placing an animal in the holding box and after 1 min, opening the door to give the animal access to the arena. A test lasted 4 min during which the following were recorded: latency (the time taken for the animal to leave the holding box), the number of grid lines crossed, and the number of defecations in the arena. Animals were tested within 48 hr of capture and always before aggression tests. An exploratory index was devised by giving each animal a rank from one to ten on each factor. The rank was obtained by dividing the range of values for each factor into ten equal groups. Animals were then assigned the value of the group in which their test value occurred. The three values for each animal were then added to give the index number. A rank of ten for latency meant that the animal emerged from the holding box very quickly. Similarly, a high rank was given for low numbers of defecations and high numbers of grid lines crossed during the test. Therefore, the higher the open

field index the greater the tendency to explore the arena without signs of emotional stress. Theoretically scores could range from zero to thirty but neither extreme occurred.

Aggression Tests

Males were given an additional test in the arena. Two males were placed in the arena, one on either side of a plywood partition. The animals were allowed to settle down for a few minutes and then the partition was removed. Animals were observed for 5 min or until they had to be separated to avoid serious injury or death of one of the animals. Each animal was rated as dominant or subordinate on the basis of posture, chasing, fleeing or biting. The level of aggressive tendency was also rated by counting the number of chases, the number of times the subordinate animal was bitten, and the number of times that self or mutual grooming took place. Each male was tested with three different animals caught at approximately the same time to avoid using individuals that had been caged for long periods. Opponents were chosen at random from untested males by drawing numbers from a hat. Aggression tests included 143 intraspecific and 18 interspecific encounters.

COLLECTING

All animals were trapped using Longworth or Sherman live traps. *C. gapperi* and *P. maniculatus* were trapped within a 10 mile radius of the Heart Lake laboratory. *C. rutilus* were trapped at Fort Providence and Fort Simpson (Fig. 1). All animals were kept in plastic cages with wire tops until used in enclosures, released or destroyed. Animals were

kept in separate cages except that females remained with their litters until the young weighed 12 g when littermates were weaned and separated. All cages were housed in an open porch of the laboratory on shelves. Cages were in close proximity but animals could not see one another. Animals used at Lacombe in September 1970 were also trapped at Heart Lake in late August and transported to Lacombe in separate cages. Animals were trapped throughout the summer from May to August 1971 to provide subjects for behavior and activity tests.

METEOROLOGY

Meteorological data were collected at Heart Lake and Lacombe throughout the test periods. Sunrise and sunset times and duration of civil twilight were taken from Berry *et al.* (1945).

Lacombe

Hourly sunshine to the nearest tenth of an hour, air temperatures, and mean hourly wind speed were recorded at the Canada Department of Agriculture Research Station 0.9 km south of the activity pens at Lacombe. Relative humidity, subnivean temperatures and snow depth were recorded within the activity pens.

Heart Lake

No record was made of the hours of sunshine or the intensity of light either above or below the snow at Heart Lake. Winter temperatures were measured 2 m above the ground and also below the snow at the soil surface in the moss. Measurement was made near the laboratory by means of thermistors connected to a Yellow Springs sequencing telethermometer

(model 47) and laboratory recorder (model 80). Summer temperature and relative humidity were recorded with a Negretti-Zambra thermohygrograph chart recorder.

Snow depth and other characteristics were measured with a snow survey kit on loan from the National Research Council of Canada (Klien *et al.* 1950). However, only snow depth is reported here and additional information is on file at the Zoology Department, University of Alberta.

Wind speed was recorded by the Mackenzie Forest Service at the edge of the escarpment with an anemometer mounted on the fire lookout tower during the summer. Measurements were also taken at ground level in the enclosures with a hand-held anemometer.

COMPUTER METHODS AND STATISTICAL TESTS

Event recorder charts were summarized by counting the number of 5-min periods per hour in which activity occurred at each location within the enclosure. Hourly activity totals were punched on IBM Fortran cards using one card per hour for each enclosure. Each card was identified with the time and place. Meteorological data were punched on the same card if space permitted or appeared on a following card.

All programs used for analysis were in Fortran IV and are on file at the Zoology Department, University of Alberta. Programs were written to summarize hourly data by day, week, 10-day period and month (10-day periods were defined as three periods, from the first to the tenth, eleventh to twentieth and twenty-first to the end of each month).

Differences in activity levels between pens and nest boxes were tested with the G-test (a goodness of fit test) reported in Sokal and

Rohlf (1969) complete with a computer program in Fortran IV. Other

statistical tests used were a simple correlation coefficient and

Student's t-test (Snedecor and Cochran 1967).

RESULTS

CORRELATION OF ENVIRONMENTAL VARIABLES WITH ACTIVITY

The first striking feature of activity was the occurrence of activity peaks about every 4 hr (Fig. 9). An activity peak was defined as the middle of three consecutive hours where activity in the middle hour was greater than that of the other two. Peaks could be a minimum of 2 hr apart where a<b>c<d>e. These short-term bursts continued throughout all seasons regardless of animal activity and were superimposed on circadian rhythms. Peaks in the short-term cycle occurred less frequently (t = 6.16, p < 0.01) in winter (Fig. 10) than in summer (Fig. 11). There was also a shift in amplitude of peaks from largest at night in summer (Fig. 12) to largest during the day in winter (Fig. 13). The figures show 10-day representative samples.

Light

The effect of sunrise on the timing of daily activity cycles at Heart Lake was evident when the total hourly activity in 10-day periods was plotted for a year (Fig. 14). Activity peaks occurred most often during the hour before sunrise. Peaks occurred again at about 4-hr intervals throughout the day with peaks becoming more erratic as the days became longer. Peaks occurring near sunset tended to get out of phase when sunset was not a multiple of 4 hr from sunrise and then shifted back in phase again. Occurrence of daily activity peaks shortly before sunrise did not change from reproductive to non-reproductive

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periods, although the type and amount of activity varied considerably. It was also noted that in April and May of 1971 at Heart Lake the number of peaks per day was reduced during the time when there was only one animal present in the pens (Fig. 14).

There was no significant correlation ($r = 0.082$, $p > 0.05$) between the number of hours of sunshine per day and total daily activity at any time of the year in Lacombe. There also was no significant correlation ($r = -0.031$, $p > 0.05$) between hours of sunshine and hourly activity during daylight. However, a greater proportion (78%) of the larger peaks occurred between 0800 hr and 2000 hr in the winter (Fig. 9), while in the summer most of the larger peaks (69%) occurred between 2000 hr and 0800 hr (Fig. 15). Once again activity peaks occurred very consistently an hour before sunrise and less consistently at sunset with additional peaks occurring approximately every 4 hr (Fig. 16). The timing of activity peaks became rather erratic during the first and third 10-day periods of January 1971. During those times the snow was deep (60 cm) and both periods had a number of days with little or no sunshine (Fig. 17).

Temperature

Results showed an unexpected relationship between activity and air temperature rather than subnivean temperature. Correlation between air temperature and total daily activity was significant ($r = 0.734$, $p < 0.01$) during the non-reproductive period (winter of 1970-71) at Heart Lake except for April (Fig. 18). The anomaly occurred during the time when predation by a weasel likely caused the observed drop in activity. There was again a significant correlation ($r = 0.675$,

p < 0.01) between air temperature and activity at Heart Lake during

September 1971 after breeding activity had ceased, at Lacombe

during the winter of 1970-71 (r = 0.712, p < 0.01) except for part of

February and March (Fig. 19) and during the winter of 1971-72 (r = 0.830,

p < 0.01; Fig. 20). There was no significant correlation (r = -0.011,

p > 0.05) between subnivean temperature and activity except during the

period when snow depth was less than 20 cm and air and subnivean

temperatures corresponded closely.

There was no difference (G = 0.043, p > 0.05) between the

temperature of insulated and non-insulated nest boxes or between nest

boxes and subnivean temperature at Lacombe. No correlation between air

temperature and activity was found during summer (reproductive period).

Snow

No correlation was found between snow depth and activity. Even

after snow depth reached 20 cm and subnivean temperature was quite

stable animals still responded to air temperature and photoperiod

Wind

No correlation was found between activity and wind speed during

either winter or summer. Although wind speed reached 40 mph above tree

level, wind within the enclosures was never found to be over 5 mph.

Relative Humidity

Correlation between relative humidity and activity was found to

be significant during two brief periods (one of 15 days, r = 0.599,

p < 0.05, the other of 10 days, r = 0.601, p < 0.05) for *Clethrionomys*

at Heart Lake during the summer of 1971 when animals were found to be

more active on days with highest himidity. Both periods were extremely

hot and dry. There was also one period (June 1971) at Lacombe when a

significant correlation (r = -0.672, p < 0.01) between humidity and

activity was found. During that time animals were most active on days

when humidity was lowest. This was during one of the wettest Junes on

record with several periods of rain lasting for 3 to 4 days and showers

occurring on most other days during the month. Activity, then, dropped

during extremes in relative humidity.

HABITAT SELECTION IN WINTER

Only *C. gapperi* were kept in enclosures during winter so no

comparison of species is possible. However, the species studied showed

a change in habitat use from one season to the next.

Heart Lake

By September 1970 at Heart Lake when breeding had ceased

activity was higher in nest boxes of pens A and D than in the others

(Fig. 21). Animals were gregarious and showed a preference for pens A

and D until the following January when use of nest boxes in other pens

at times exceeded that of A and D. Use of feeders declined throughout

the winter, ultimately ceasing in late winter. Feeders were found to

be badly fouled by feces and sunflower seed shells in spring.

Lacombe

When animals were released at Lacombe in September of 1970,

breeding activity had already ended and animals were usually found in

groups of three to six individuals whenever a census was taken.

Preference was shown for the nest boxes of pen A throughout the winter and spring of 1971 (Fig. 22) until a female became pregnant and defended that pen as a territory (see Habitat Selection in Summer). Nest boxes within pen A were used about equally with each used for a few days at a time.

Feeders were utilized throughout the winter; however, the use of the feeder in pen A did not correspond to the use of nest boxes in the same pen. Rather, the animals seemed to use only one feeder at a time (Fig. 23) plugging the other two with snow. There was no evidence that animals attempted to move into feeders for nesting purposes. Very little food storage in nest boxes occurred in Lacombe prior to the winter of 1970-71. In September 1971 several nest boxes in each pen had some food stored in them with one nest box in pen C filled.

WINTER MORTALITY

Heart Lake

During the winter of 1970-71 only one animal (a female) out of the original 24 animals survived at Heart Lake. Since it was not possible to take a census without disturbing the snow cover there was no direct evidence to show when or how the 23 animals disappeared over the winter. Snowfall was light during the first part of the winter of 1970-71 at Heart Lake. A depth of 20 cm was first attained in early January. The spring melt occurred in April and was of short duration (Fig. 18).

There were indications that predators may have taken some animals from the enclosures during the first winter. The expected rise in

activity following a rise in air temperature (see Effects of Environmental Variables) did not occur after a weasel was seen in the enclosure at the end of January (Fig. 18). There was another sharp drop in activity at the end of March and a third drop in mid-April, both following visits by a weasel.

One dead animal was recovered from a nest box in which it had apparently become trapped when the swinging door froze shut as a result of water running into the switch housing.

In September of 1971 eight animals were left in each of the enclosures at Heart Lake. However, predation by a stray cat (*Felis domestica*) completely exterminated the population by 26 September before there was any snow on the ground.

Lacombe

There was no winter mortality at Lacombe during the winter of 1970-71. It should be noted that screens prevented predation in these pens. Snowfall was also earlier than at Heart Lake reaching a depth of 20 cm by late November. Snow was exceptionally deep (for that area) reaching 60 cm, necessitating removal of some snow from the enclosure to prevent the escape of animals. The spring melt occurred rapidly during the first week in April (Fig. 19). There was an unexplained drop in activity at the end of January and during February corresponding to a drop at Heart Lake but recovery was complete by the time the snow disappeared.

Survival at Lacombe during the winter of 1971-72 was considerably better than winter survival at Heart Lake for the comparable time. Twelve animals remained in the pens at the end of September when breeding

activity ended with a subsequent decline to seven animals by the following spring. Survivors included two animals from litter two and five animals from litter three (Fig. 25).

In the latter part of October 1971 three animals apparently died of cold. They showed no signs of aggression and were not trapped in the nest boxes in any way. However, those animals were the last survivors of the original six put into the pens in October 1970. Another two animals died during the winter when they became trapped (one in a feeder, the other in a nest box). In both cases after the animal entered the passageway it was plugged from the outside with snow and the metal door prevented removal of the snow from the inside.

The winter of 1971-72 at Lacombe had less snow than the previous winter. A depth of 20 cm was first reached in late December and the spring melt was earlier ending in mid-March (Fig. 20). One exceptionally heavy snowfall in early March required the removal of a small amount to prevent the escape of animals from the enclosure.

HABITAT SELECTION IN SUMMER

During the spring and summer one pen of each unit (mostly pens A and D) was defended by a pregnant or lactating female which was found to be dominant over all other animals in the unit. Activity usually dropped in the defended area until the litter was weaned (Fig. 24). The largest male was next in the hierarchy but did not defend a territory. The remaining animals were grouped at the bottom staying in the least favorable part of the habitat most of the time. Death from aggression was highest among males and juveniles during the summer (Fig. 25).

Lacombe

In the spring of 1971 dispersal (breakup of animals from their gregarious winter condition) occurred simultaneously with the onset of fighting among males. One male (No. 14) was assumed to be dominant over the other males when one was found dead (No. 2) and the other (No. 9) had very rough looking pelage and was seen to retreat whenever approached by No. 14 (Table 3). No. 14 was also seen in pen A more often than the other males (Table 1). Male No. 2 was found on autopsy to have 50 holes in its hide, presumably a result of bites by other voles. The dominance of No. 14 appeared to continue as male No. 9 again with numerous bite marks all over its hide died 2 wk after the second litter was born, that is, 1 wk after the time when female No. 31 probably conceived her third litter.

Females tended to use separate nest boxes during the first 2 wk after the snow melted but without any signs of aggression. About 2 wk before the first litter was born one of the females (No. 31) showed strong territorial behavior excluding all animals but the dominant male from pen A. About a week before the litter was born even that male was excluded. Evidence came from encounters observed in the pens (Table 3) and from daily censuses (Table 2).

About 2.5 to 3 wk after they were born members of the first litter began to emerge from their nest box. At first they were found only in pen A. Gradually they began to use the other pens but were still observed only in the nest boxes of pen A whenever a census was taken.

A week after the second litter was born in pen A to No. 31 she suddenly became aggressive towards her first litter which then moved to

pen B. One young female (No. 51), later killed by No. 31 in pen A, was found to be pregnant (embryos just visible). Another female of the first litter (No. 50) disappeared and was presumed eaten during the first week after it was forced to leave pen A. The remaining members of the first litter were seen in pen A a few times and were chased out of the pen by No. 31 like any other animal (see Behavior).

A few days before the third litter was born in pen A the second litter moved to pens B and C. Within 1 wk two of these disappeared and were presumed eaten. When the third litter was weaned in the first week of August they also moved to pens B and C. However, at this point the activity in pen A showed a marked increase while activity in the ports between pens showed a decrease (Fig. 26), indicating additional animals were occupying nests in pen A. The social structure broke down and even No. 31 failed to raise the litter which was born in pen A at that time. On 4 September one of the old females (No. 22) was found dead in pen A with numerous holes in her pelt but it could not be determined if she was pregnant. At this point 12 animals of various ages remained (Fig. 25). Census data after 7 September showed animals to be gregarious again and birth of a sixth litter to No. 30 on 26 September was not accompanied by any marked shift in activity between pens (Fig. 26). The number of animals in the last litter was not determined as they were partially eaten when discovered.

Heart Lake

During August 1970 when animals were first introduced into the enclosure at Heart Lake, breeding activity had not yet ended. At that time pens A and D were being defended by pregnant females (see

Habitat Selection in Summer), resulting in lower activity in pens A and D than in other pens (Fig. 21).

At the start of each of the six tests in the old and new pens at Heart Lake in the summer of 1971 the animals sorted themselves out so that a female occupied pen A or D usually excluding all other animals except for a few cases where a male shared the pen with a female for at least part of the time. The dominant female defended the pen by advancing on any intruder that ventured into her territory. Usually the intruder fled at first sight of the dominant female. In a few cases the female bit the intruder on the rump.

Animals that did not use the nest boxes in pen A or D were found most often in pens C and F but also occasionally in pens B and E. With few exceptions only one animal was found per nest box during a census.

Because of the short duration of each test only one litter was weaned while in the enclosures. The results were similar to those at Lacombe. The young moved to pen B and subsequently to pen C after being attacked by their mother who was later found to be pregnant (embryos 1.5 mm long) when autopsied.

Females were considered dominant if they chased animals more often than they were chased by others. There was seldom difficulty in distinguishing which female was dominant and once the rank was established it seldom changed. Dominant females were usually found to have fewer bite marks on the pelt at autopsy and were either pregnant or lactating (Tables 4 and 5).

Males were killed more often than females although they did not defend territories. Evidence of aggression in the enclosures came

mostly from the autopsies as fights were rarely seen (Tables 4 and 5). Consequently, males were classified as dominant if they received few injuries and were found in pen A or D more often than in other pens during daily censuses.

BEHAVIOR

C. gapperi and *C. rutilus* were found to be more similar in many respects than *C. gapperi* and *P. maniculatus*. Daily activity patterns of both *Clethrionomys* were about the same with *C. rutilus* a little less active. *P. maniculatus*, however, was quite different having a bimodal, nocturnal pattern of activity (Fig. 27).

Open Field Tests

There was a significant difference between average scores of *C. gapperi* males and females (t = 2.35, p < 0.05). *C. gapperi* juveniles had higher average scores than adults (t = 2.40, p < 0.05). There was no difference (t = 0.94, p > 0.05) between *C. gapperi* juveniles raised in cages and those caught in the wild. Numbers of *C. rutilus* and *P. maniculatus* were deemed too small to use statistical tests. Within females of each class, lactating animals had highest scores while pregnant animals (especially near parturition) had lowest, resulting in the greater range of values for females in every class in Table 6. *C. gapperi* had the highest average scores followed by *P. maniculatus* and *C. rutilus*. No relationship was detected between open field scores of females and success in obtaining a territory.

Aggression Tests

The numbers of interspecific tests between males (7 *P. maniculatus* vs. *C. gapperi* and 11 *C. gapperi* vs. *C. rutilus*) were too low to show statistical significance. However, some trends were noted. Heaviest animals tended to be dominant in every class (Table 7). Contests between different genera showed the lowest level of aggression, between members of the same species showed the highest level of aggression while different species of the same genus were intermediate. No change was detected in level of aggression throughout the season. *C. gapperi* showed more intraspecific aggression than *C. rutilus*.

Interspecific Interactions

Results of a single test showed that a *C. gapperi* female and a *P. maniculatus* female simultaneously used the same pen while raising litters. The *C. gapperi* female moved her 3-day-old litter into the pen occupied by the *P. maniculatus* female. Animals of both species showed avoidance reactions when meeting but this occurred only when animals of different species approached each other closely as when meeting in a tunnel. No agonistic encounters or chasing of one species by the other was observed. When the port between units of the enclosure was opened the level of activity for nests in pen D (where *P. maniculatus* was established) increased and remained higher while activity for the feeder in pen D increased for a day and then returned to its former level (Fig. 28). This pattern would be accounted for if the *C. gapperi* female that established a nest in pen D continued to use the feeder in pen A.

When *C. gapperi* and *C. rutilus* were allowed access to each other's areas in an enclosure, *C. gapperi* were always first to cross to

the other side. Again no interspecific aggression was observed but it
could easily have occurred undetected. Strong avoidance reactions were
shown by both species. On a few occasions even relatively distant
sightings (2 m) resulted in the intruder fleeing back to its own side
of the enclosure. Of the five tests conducted, four showed an increase
in activity in the feeder and nest boxes of the *C. rutilus* side and a
decrease in activity on the *C. gapperi* side (Fig. 29). In the fifth
test both sides showed an unexplained decrease in activity with *C.
gapperi* having the greatest drop (Fig. 30).

Once a female of either species had established a territory in
pen A or D members of the other species were not able to displace it.
There were also no incidents of two females of different species of
Clethrionomys sharing a pen. However, *C. rutilus* females lost 75
percent (three out of four) of their litters during tests compared to
20 percent (one out of five) litter loss by *C. gapperi* during the
comparable time. A litter was considered successfully raised if at
least one animal remained healthy until weaning or the end of the test.

DISCUSSION

ACTIVITY CYCLES AND ENVIRONMENTAL VARIABLES

Short-Term Rhythm

The short-term (2 to 5 hr) cycle in activity has been previously
reported as a feeding cycle (Miller 1955). The constancy of this
pattern of activity throughout all seasons strongly supports the
feeding theory especially since feeders were used regularly where food
was not stored in nest boxes. Moreover, the 2 to 5 hr cycle continued
even when the diurnal rhythm lost its synchrony with sunrise in
January 1971 at Lacombe. Brown *et al.* (1970) have suggested a cellular,
biophysical model to explain timing of some short-term cycles that
could not be correlated with any external cues. This is contrary to
the view of Enright (1965) and Bruce (1960) who claim that all
endogenous cycles are synchronized by environmental influences which
are often just undetected. Although no attempt was made to show that
timing of short-term activity cycles was endogenous, it tends to fit
the cellular, biophysical model of Brown *et al.* (1970). Bünning (1964)
suggested that social synchronizers are very important to mammals. If
the short-term rhythm is endogenous then the change in behavior from
summer to winter would be sufficient to cause the observed change in
cycle interval. It appears that sunrise is the most important event in
adjusting the 2 to 5 hr cycle so that some of the peaks form a circadian
rhythm.

There is a possibility that the short-term activity rhythm found in the present study is really random fluctuation. It has been shown by Cole (1954) that random numbers grouped in threes (a, b, c) can be arranged in six possible ways and that two of these arrangements will have b in the middle. Therefore, in an infinite series of numbers, peaks defined as a<b>c will occur on the average approximately one out of three times. Cycle intervals in the present study are about what would be predicted by chance, that is between 3 and 4 hr. This could possibly be resolved by defining peaks as a<b<c>d>e. However, this would mean peaks could occur at a minimum of every 4 hr and any real fluctuations with a smaller interval would not be detected. There is also the concomitant problem of differentiating between major and minor peaks whenever fluctuations vary widely.

Circadian Rhythm

Seasonal variation in circadian rhythm of *C. gapperi* was found to be related to a number of environmental variables. It was found that sunrise had a synchronizing effect on short-term activity peaks. The loss of synchrony with sunrise during January 1971 was probably caused by inability of the animals to recognize sunrise under conditions of deep snow and little or no sunshine.

Differences between Lacombe and Heart Lake circadian rhythms are likely due to latitude. At the summer solstice Heart Lake had a period of darkness of about 2.5 hr while at Lacombe darkness always exceeded 4 hr. This would indicate that circadian rhythm is adjusted to local conditions. Calhoun (1945) found two other species of

voles to have diel, bimodal rhythms that were easily affected by light, temperature, food and breeding behavior, while Buchalczyk (1964) found that *Apodemus flavicollis* inhibited nighttime activity of *C. glareolus* where both species were present.

The shift from heavy activity in the daytime in winter to heavy activity at night in summer has also been found in *Microtus agrestis* by Erkinaro (1961). It has been suggested that the seasonal adjustment of a diurnal clock to certain environmental factors has adaptive advantages such as avoidance of adverse temperatures and predators (Bünning 1964). Differences between summer and winter diel rhythms suggest that *Clethrionomys* avoid the hottest daytime temperatures during the summer while taking advantage of the warmest part of the day during the winter. The winter snow cover gives protection from at least airborne predators and may facilitate this shift.

Correlation of activity with other environmental variables ranged widely. The lack of correlation with wind speed was not unexpected as there was little wind in the enclosures.

The unexpected positive corrleation with air temperature in winter shows that small mammals are more aware of conditions above the snow than was previously suspected. The lack of correlation with subnivean temperature is unexplained. The reduced correlation of air temperature with activity in summer suggests that either temperature variation is not important, or it is overshadowed by other stimuli (such as breeding and litter raising). It is suspected that the latter could be shown by measuring the activity of solitary animals in the summer temperature range. There is probably an optimum

temperature above which activity would again decrease.

The unusual correlation between relative humidity and activity again suggests an optimum level of humidity at which animals are most active.

HABITAT SELECTION IN WINTER

The habitat gradient used in this study was not intended to represent major habitat differences found in the wild. Rather, it was meant to provide animals with some choice in living conditions within their normal habitat. It was concluded from the activity data that animals preferred some part of the enclosure over others through-out the year. In winter pens A and D were preferred by most animals. Use of other pens at Heart Lake was most likely due to the large quantities of food stored in nest boxes during the previous fall. The large number of animals may also have caused excessive fouling of nest boxes in pens A and D early in the winter, forcing a move to cleaner quarters. The pattern of use of nest boxes within a pen suggests that they were often used in rotation and may have been a behavior pattern to avoid buildup of feces, moisture or ectoparasites (none were found during handling of the animals except when caught in the wild).

Winter preference for pens A and D was not likely due to the presence of feeders and may have been due to insulation but more likely due to the size of the nest boxes. The important point is

that animals used only a part of the available habitat at one time by clumping together.

WINTER MORTALITY

Winter survival of small rodents may depend on spring and fall critical periods (Fuller 1967), severe mid-winter temperatures (Beer 1961), and disease and predation by birds and mammals (Hatt 1930). In the present study predation by weasels appeared to be the most important factor in reducing the 1970-71 winter population at Heart Lake. Beer (1961) also noted many predators in his study area but considered them unimportant to mammals under the snow.

Death during the spring melt was of secondary importance and may have been even more severe in the enclosures than in the wild due to the danger of mechanical equipment being frozen and the fact that animals were prevented from moving to more favorable areas if the enclosures became uninhabitable.

In Lacombe where predation was eliminated, mortality was also eliminated during the first winter and was low the second. However, during the second winter when mortality was higher the snow came later in fall and melted earlier in the spring. Deaths due to natural causes occurred in fall before there was snow on the ground.

Mortality in the wild would most likely be caused by a combination of many factors including food shortage which was never a problem in the enclosures. Extrapolation to the wild from the enclosures is difficult and predation is probably less important in

the wild than in the enclosures.

HABITAT SELECTION IN SUMMER

Activity data show that animals again favored the "good" habitat in summer. The lower level of activity from time to time in pens A and D does not indicate a lack of preference when behavior is taken into account. Preference for the "good" pens by pregnant and lactating females is shown by the percentage of litters that were raised there.

It would appear that females need a territory to successfully raise litters. This territory can be fairly small, probably only the immediate area around the nest in the wild if the size of territory in the enclosures is any indication. Getz (1961) found that *Microtus* females had a territory about 7 m in diameter which was a small part of its home range. Territorial behavior prevented a large part of the population from using the "good" habitat until social structure broke down.

It is unlikely that the presence of a feeder was important in the choice of a territory; however, the provision of three feeders at Lacombe probably allowed the population to reach a higher level before it declined. The size of the nest boxes in pens A and D was probably more important to animals when choosing those areas. Brown (1953) found that litters of house mice were successfully raised only in large, completely enclosed nests.

The fact that males tend to move around more in summer than females suggests that males have a larger home range than females and do not exhibit territorial behavior to the same extent as suggested by Getz (1961) for *Microtus*.

Failure to raise litters to maturity in the fall of 1970 at Heart Lake could have been caused by an excessive number of animals competing for one feeder located in the "good" habitat. There is also a possibility that during the fall of 1970 and summer of 1971 animals showed excessive aggression in the enclosures because of their recent introduction from different areas. Healey (1967) suggested that animals react more aggressively towards strange individuals from outside their immediate neighborhood.

Densities in enclosures were 900 to 4,800 animals per acre or 150 to 1,200 times those observed concurrently in nature (Fuller, pers. comm.). Social interaction is likely unimportant in nature unless: (1) populations are clumped, or (2) there is a shortage of suitable nesting territories. Getz (1961) found summer populations of *Microtus* clumped but believed density to be unimportant in animal distribution. This was rejected by Chitty (1964) who suggested that the uneven distribution of small mammals is an important factor leading to social interactions and consequently population regulation.

BEHAVIOR

Open field tests seemed to be a good indicator of willingness to explore surroundings and perhaps to emigrate except for females that were pregnant or lactating. Care should be exercised when interpreting results from adult females as test values changed rapidly with changing reproductive condition. The higher values of the males agree with their reported larger home range (Getz 1961, Bodner, pers. comm.). The lower values for *C. rutilus* males may be unreliable due to the small sample size. Further work is also needed to determine whether open field scores change from summer to winter to correspond with the activity level found in the enclosure.

Aggression tests were made to show relationships within and between species used during the course of this study. Results indicated that aggression was highest between males of the same species and lowest between males of different genera. It is not known if this trend would hold for females and it would be difficult to test since female behavior changes radically during pregnancy and lactation.

Dominance shown by heavier animals over lighter ones supports most findings that juveniles cannot compete successfully with adults when becoming established in new areas.

The dominance of *C. gapperi* over *C. rutilus* may not be due to species difference because in each of the few tests *C. rutilus* males were a little lighter. Lack of animals limited further testing. The results show mutual avoidance between species which could be important in keeping *C. gapperi* and *C. rutilus* separated at the boundary between their ranges. Since *C. gapperi* and *P. maniculatus* have different ecological

niches, mutual avoidance is probably of less importance or perhaps serves a different function in this case.

Intraspecific Interactions

The aggressive nature of adults during the summer in all species studied indicated that this would be the most likely time for dispersal. It was further indicated that males and juveniles are forced to move to new and possibly less favorable areas. Expulsion of litters by mothers from their territories and failure to recruit juveniles into the breeding population agrees with the finding of others that juveniles are subordinate to adults (Watts 1970, in *Clethrionomys*; Healey 1967, in *Peromyscus*; Brown 1953, in *Mus*). Each species seems to send its least aggressive members out to new areas when suitable nesting space is least likely to be available especially during a population peak. This probably results in an annual population level in excess of the number that can successfully breed and raise litters in any given area.

The sudden change to gregarious behavior in fall and winter allows a larger number of animals (including juveniles) to overwinter allowing high winter mortality in one area to be compensated by dispersal from an adjacent area the following spring. The formation of groups in winter also allows animals to conserve heat by reducing surface to volume ratio by huddling during periods of rest. The absence of agonistic behavior in winter allows animals to congregate in better areas and thus avoid areas of light snow cover (Pruitt 1957, Beer 1961).

Interspecific Interactions

Results of the present study indicate that *C. gapperi* may raise litters at higher population densities, show more agression, and be more

prone to enter and explore another species' territory than *C. rutilus*.
However, Murie (1972) found *C. rutilus* rather than *C. gapperi* to be
dominant in enclosures. This difference may be due to random selection
of animals and small sample sizes or because of cyclic behavioral
changes in the animals as Krebs (1970) and Chitty (1964) have suggested.
Furthermore, limited data indicate that *C. rutilus* have crossed the
Kakisa River more often than *C. gapperi* (Fuller 1969). The low incidence
of crossing may be due to the gregarious nature of *C. gapperi* and
probably also *C. rutilus* in winter when the Kakisa River is frozen and
easily crossed, while both species have shown more inclination to
disperse when the Kakisa River is open and difficult to cross. Further
research is needed to resolve these differences.

Earlier hypotheses have suggested that physiologic differences
are responsible for the present distribution of *C. gapperi* and *C. rutilus*
(Fuller 1969, Murie 1972). It seems unlikely that there are any
environmental differences across the narrow boundary separating the two
species to give one species a selective advantage on one side but not
on the other. To date it has not been shown that the boundary between
these species follows any climatic, vegetative or soil substrate
boundary.

Ayala (1972) has shown that contrary to the principle of
competitive exclusion, two or more species of *Drosophila* competing for
the same resources can permanently coexist. *C. gapperi* and *C. rutilus*
like the above sibling species are very similar and if sympatric would
probably compete for the same resources. Behavioral differences shown
by the present study and by Murie (1972) seem to be sufficient to prevent

cross breeding in nature and probably affect the regulation of densities within species.

It is speculated that mutual avoidance may be the mechanism keeping the two species of *Clethrionomys* apart and that this is enhanced by a barrier that limits the numbers crossing with the result that emigrating individuals will be outnumbered by the other species. The failure of one species to displace the other within the enclosure supports the hypothesis of mutual exclusion between *C. gapperi* and *C. rutilus*. However, even a minor behavioral shift could upset the delicate balance allowing one species to displace the other, permit the two to live sympatrically in different niches or even allow both species to occupy the same niche as Ayala (1972) found in *Drosophila*.

Although the ultimate limit of the range of each species is probably governed by physiological characters, the proximal factors in this situation seem more likely to be behavioral manifested as competitive exclusion. Further research is required to confirm whether the present hypothesis best explains the allopatry of *C. gapperi* and *C. rutilus*.

but the hypothesis of mutual exclusion based on interactions in

enclosures and limited aggression tests seemed at least as good as other

proposals.

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TABLES

Table 1. Results of daily morning censuses of *C. gapperi*, April to September 1971, showing the number of times that males were found in each pen during 10-day periods at Lacombe

An. No.	Pen	Apr.			May			June			July			Aug.			Sept.		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	A	8	7	6	2	5	0	0	3	3	–	0	0	3	5	5	3	4	3
14	B	1	2	3	6	3	4	7	4	4	–	6	7	4	3	4	3	3	4
	C	0	1	0	0	1	2	2	1	1	–	2	3	3	1	0	3	2	1
	A	6	6	4															
2	B	2	3	5	Died April 28														
	C	1	1	0															
	A	7	4	0	1	0	0	1	2	3									
9	B	0	5	3	2	1	1	1	4	1	Died June 28								
	C	2	1	6	5	8	5	7	2	1									

Table 2. Results of daily morning censuses of *C. gapperi*, April to September 1971, showing the number of times that females were found in each pen during 10-day periods at Lacombe

An. No.	Pen	Apr.			May			June			July			Aug.			Sept.		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
	A	9	10	9	8	9	6	8	8	7	–	8	10	8	6	5	3	6	4
31	B	0	0	0	0	0	0	1	0	1	–	0	0	2	3	3	4	2	2
	C	0	0	0	0	0	0	0	0	0	–	0	0	0	0	1	2	1	2
	A	6	0	0	0	0	1	0	1	0	–	0	0	1	2	3	3	4	2
22	B	3	7	8	8	4	5	8	7	6	–	8	8	5	7	6	3	3	2
	C	0	3	1	0	5	0	1	0	2	–	0	2	4	0	0	3	2	4
	A	5	0	0	0	0	0	0	0	1	–	0	0	0	1	2	2	3	2
30	B	4	0	2	4	4	2	0	0	1	–	1	3	1	7	1	3	3	2
	C	0	10	7	4	5	4	9	8	6	–	7	7	9	1	6	4	3	4

Table 3. Number and kind of intraspecific encounters, reproductive
success and signs of fighting in *C. gapperi* at Lacombe,
April to September 1971

An. No.	Sex	Encounters			No. of litters		Holes in pelt
		Neut.	Dom.	Sub.	Born	Weaned	
31	F	18	89	0	4	3	7
22	F	46	14	11	1	0	41
30	F	27	1	32	1	0	22
14	M	21	66	19	–	–	11
2	M	6	2	22	–	–	50
9	M	30	12	42	–	–	57

Table 4. Number and kind of intraspecific encounters, reproductive success, signs of fighting and weight of animals in the first Heart Lake enclosure, June to August 1971

Test	An. No.	Sex	Encounters Neut.	Dom.	Sub.	Reproductive condition	Holes in pelt	wt. (gm)
	P 1	M	32	20	7	Test.+	0	27
	P 2	M	0	0	35	Test.+	35	22
	P 6	F	1	0	18	Killed (no autopsy)	–	25
	P13	F	31	40	0	Preg./Lact.	0	28
1								
	G 5	M	3	10	1	Test.+	3	28
	G19	M	4	0	12	Test.+	26	25
	G13	F	2	0	1	N. br.	20	28
	G18	F	1	4	0	Preg./8mm embryos	2	26
	G 7	M	0	0	1	Test.+	0	23
	G20	M	2	2	1	Test.+	1	22
	G16	F	0	0	6	N. br.	2	26
	G33	F	2	8	0	Preg./Embryos just vis.	0	28
2								
	R 2	M	2	0	12	Test.+	42	18
	R 4	M	1	3	1	Test.+	11	18
	R15	F	3	0	8	N. br.	38	16
	R17	F	2	18	0	Preg./(probably)	6	18
	G38	M	3	0	11	No autopsy	–	32
	G49	M	1	4	0	No autopsy	–	23
	G50	F	0	0	5	No autopsy	–	19
	G57	F	2	12	0	Preg.	–	32
3								
	R25	M	6	0	1	No autopsy	–	16
	R26	M	7	0	1	No autopsy	–	17
	R 3	F	8	1	0	No autopsy	–	20
	R12	F	5	0	1	No autopsy	–	20

P = *P. maniculatus*, G = *C. gapperi*, R = *C. rutilus*, Test.+ = sperm present, Preg. = pregnant, Lact. = lactating, N. br. = no breeding.

Table 5. Number and kind of intraspecific encounters, reproductive

success, signs of fighting and weight of animals in the

second Heart Lake enclosure, June to August 1971

Test	An. No.	Sex	Encounters Neut.	Dom.	Sub.	Reproductive condition	Holes in pelt	wt. (gm)
	G 3	M	3	6	1	Test.+	14	25
	G 6	M	0	0	8	Test.+/(killed)	12	25
	G 4	F	0	11	10	Lact.	4	22
	G22	F	3	10	8	Preg.	14	28
1								
	R 6	M	6	0	1	Test.+	0	24
	R 7	F	3	7	2	Preg.	5	19
	R9	F	3	2	6	Lact./(litter killed)	10	26
	G29	M	10	2	1	Test.+	4	20
	G35	M	1	0	2	Test.+/(killed)	40	21
	G28	F	3	0	6	N. br.	3	18
	G45	F	8	5	0	Preg.	3	26
2								
	R10	M	4	2	1	Test.+	10	24
	R21	M	3	2	2	Test.+	16	25
	R 8	F	7	1	8	Preg.	8	23
	R22	F	3	6	0	Preg./(litter killed)	31	23
	G40	M	7	4	1	No autopsy	–	16
	G59	M	11	2	1	No autopsy	–	19
	G54	F	10	0	9	No autopsy		19
	G56	F	2	11	0	Lact.	–	35
3								
	R11	M	2	1	0	No autopsy	–	23
	R28	M	6	0	1	No autopsy	–	18
	R19	F	7	2	0	No autopsy	–	21
	R23	F	4	0	2	No autopsy	–	17

G = *C. gapperi*, R = *C. rutilus*, Test.+ = sperm present, Preg. =
pregnant, Lact. = lactating, N. br. = no breeding.

Table 6. Open field test scores

| | Overwintered | | Juveniles | | | | Total | | |
| | | | Captive | | Wild | | | | |
	M	F	M	F	M	F	M	F	MF
P. maniculatus									
No. of tests	7	5					7	5	12
Range	7-16	5-19					7-16	5-19	5-19
Mean	14.7	11.0					14.7	11.0	12.2
C. gapperi									
No. of tests	24	15	12	9	7	3	43	27	70
Range	4-19	3-23	16-23	6-24	14-24	10-26	4-24	3-26	3-26
Mean	16.0	12.1	20.9	18.3	19.6	16.9	18.3	13.8	16.8
C. rutilus									
No. of tests	4	7	5	8	4	2	13	17	30
Range	2-8	1-21	10-18	2-20	4-13	6-20	2-18	1-21	1-21
Mean	6.8	9.2	13.2	13.7	9.0	11.3	9.1	11.6	10.5

M = male, F = female, for significance of differences between means see text.

Values are an index based on summing scores for latency, lines crossed in the arena and number of defecations (see text).

Table 7. Summary of outcome of aggression tests

Species A	Species B	Times A won	Times B won	Number no cont.	Total contests	No. won by heavier animal	No. won by lighter animal	% no cont.
P. maniculatus	P. maniculatus	-	-	2	14	10	2	14
C. gapperi	P. maniculatus	0	0	7	7	0	0	100
C. gapperi	C. rutilus	3*	1	7	11	3	1	63
C. gapperi	C. gapperi	-	-	13	107	83	11	12
C. rutilus	C. rutilus	-	-	4	22	16	2	18

No cont. = no fighting occurred.

*This difference was probably a case of the heavier animal winning 3/4 of the encounters.

FIGURES

Figure 1. Map of study areas

       A - Shows relative size and location

       B - Detail of area around Heart Lake

       1 - Heart Lake laboratory

       2 - Fort Providence

       3 - Fort Simpson

       4 - Kakisa River

       5 - Lacombe

       6 - Hay River

       7 - Edmonton
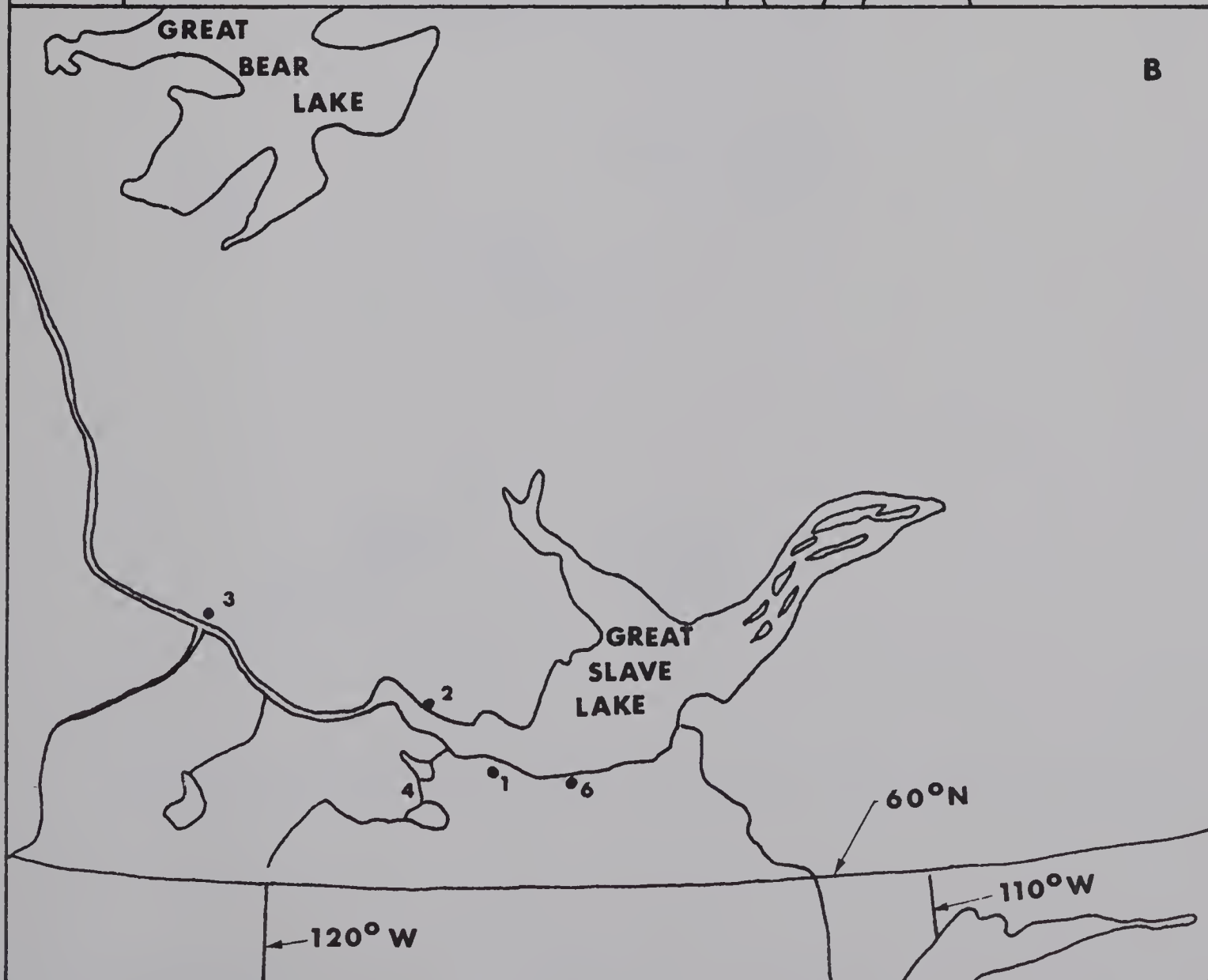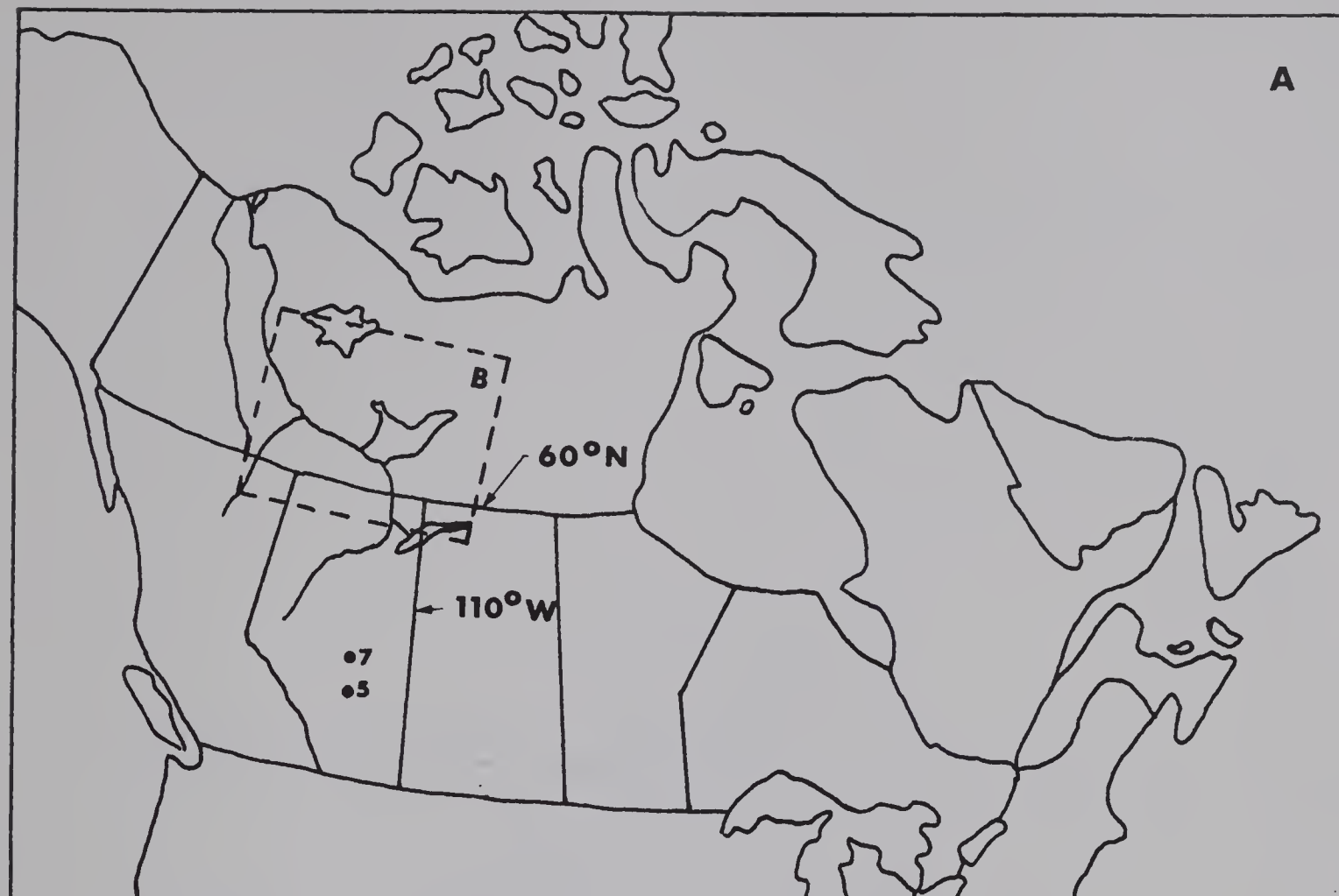
Figure 2.   Plan of Heart Lake Biological Station, University of Alberta

1 - First Heart Lake enclosure

2 - Second Heart Lake enclosure

3 - Laboratory

4 - Living quarters

5 - Access road

10 m

1

2

3

4

5

N
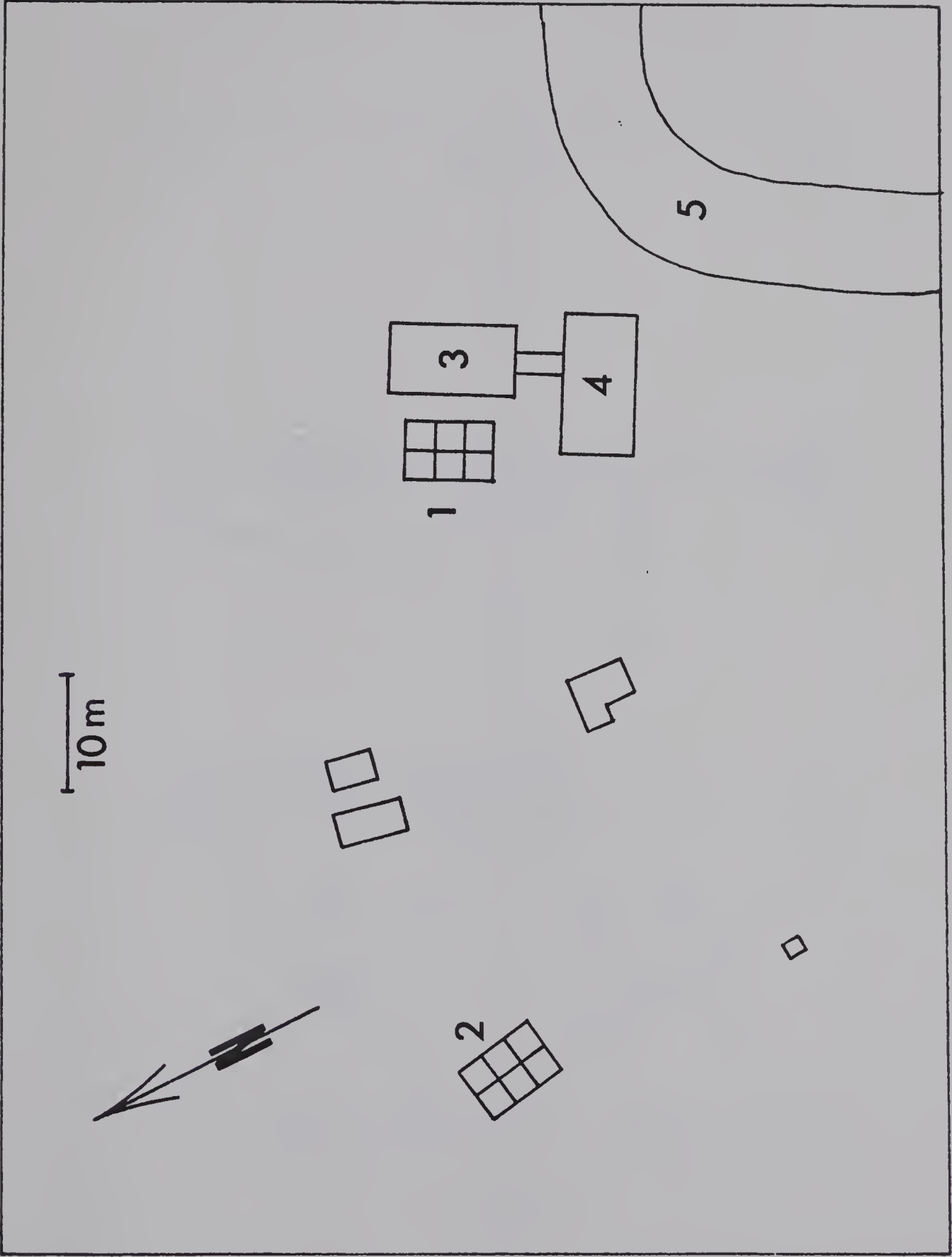
Figure 3. First Heart Lake enclosure

▲ conifer tree (15 cm diameter)

□ nest box

[F] feeder

⊏⊐ tunnel

○ entrance passageway with
    mercury microswitch

PEN F PEN C

PEN E PEN B

F F

PEN D PEN A
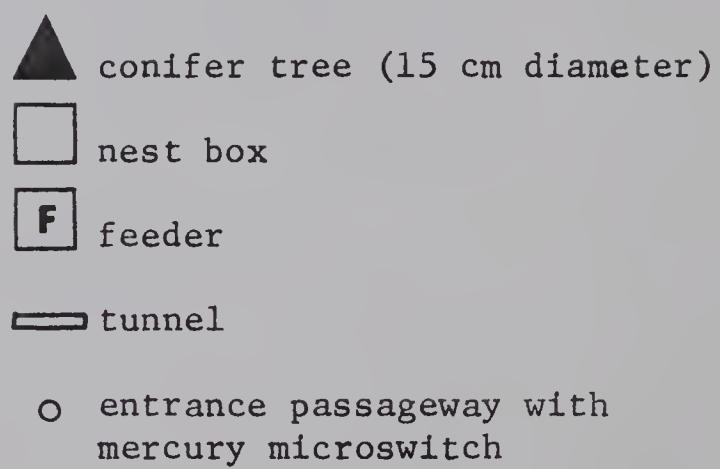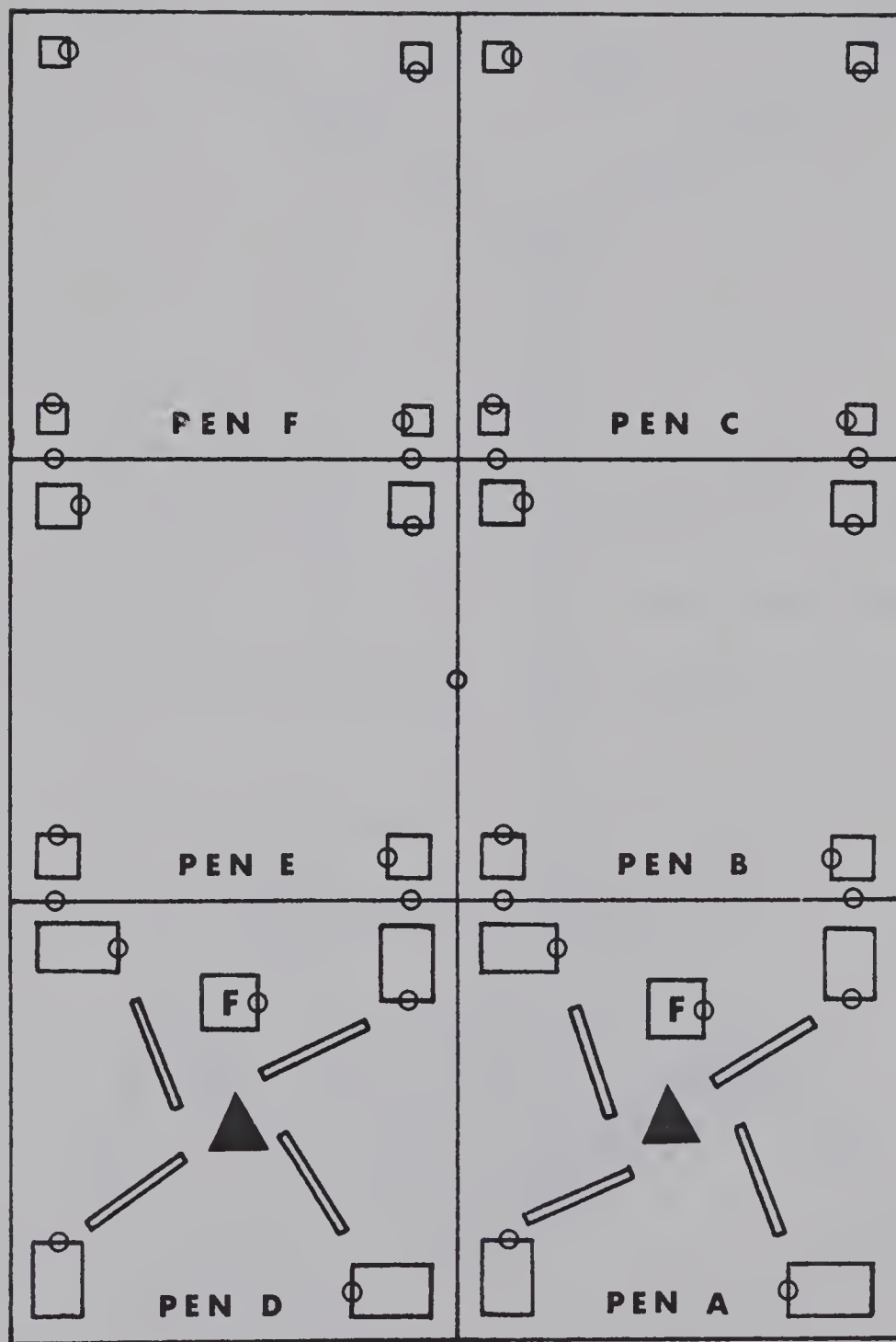
├─────────┤
1 m

Figure 4. Cutaway view of self-feeder used in enclosures. Construction
was of 6 mm plywood sides and 12 mm plywood base. A lid of
galvanized sheet metal (not shown) was placed on top to
exclude rain and snow. Feeder and base could be separated for
cleaning.

A - Compartment for sunflower seeds

B - Compartment for Rockland Mouse/Rat Diet

A

B

10 cm
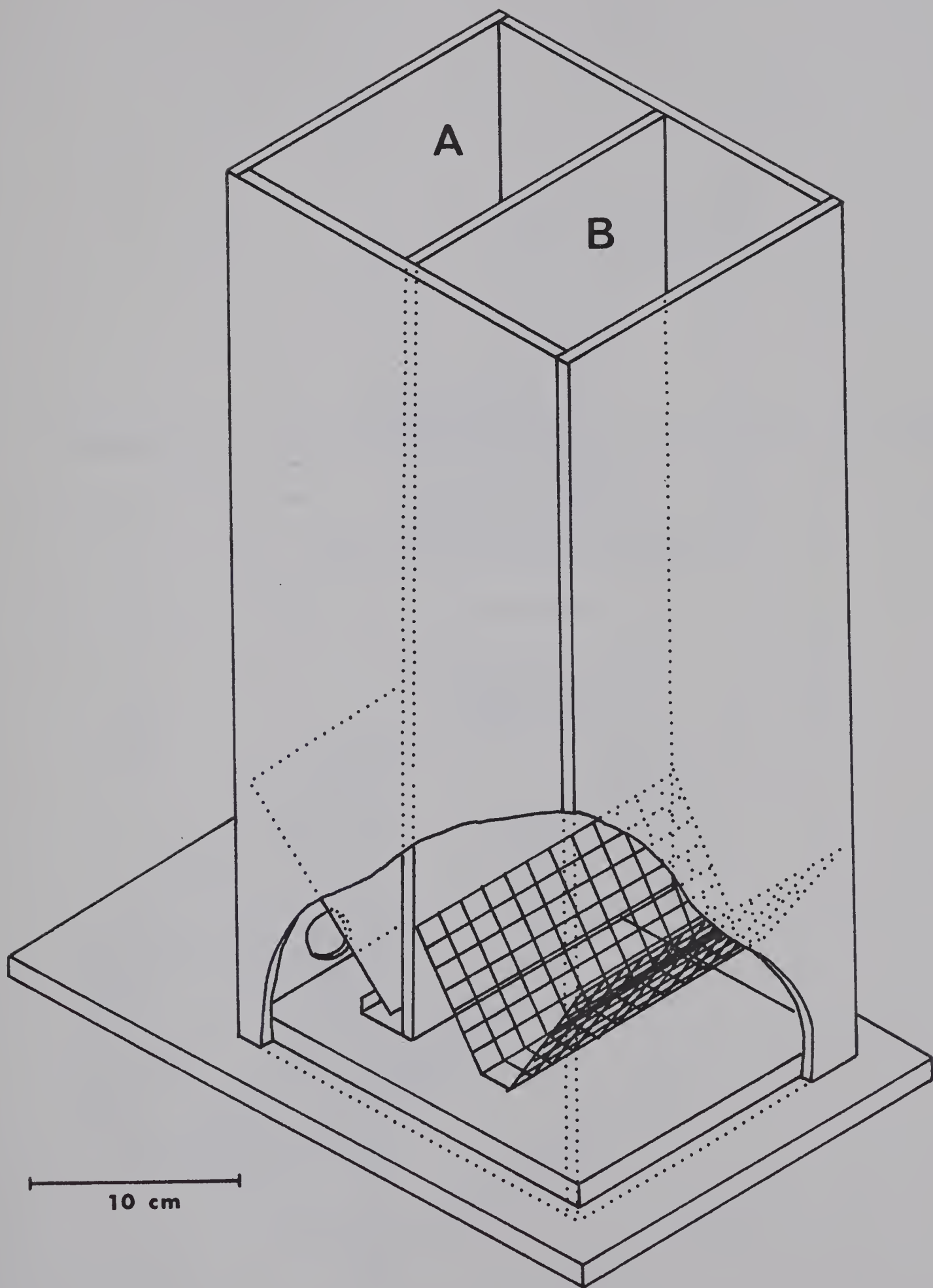
Figure 5. Cutaway view of entrance passageway and switch assembly

A - Front elevation

B - Oblique cutaway view

1 - Swinging door

2 - Mercury switch

3 - Metal ramp

A

B

5 cm
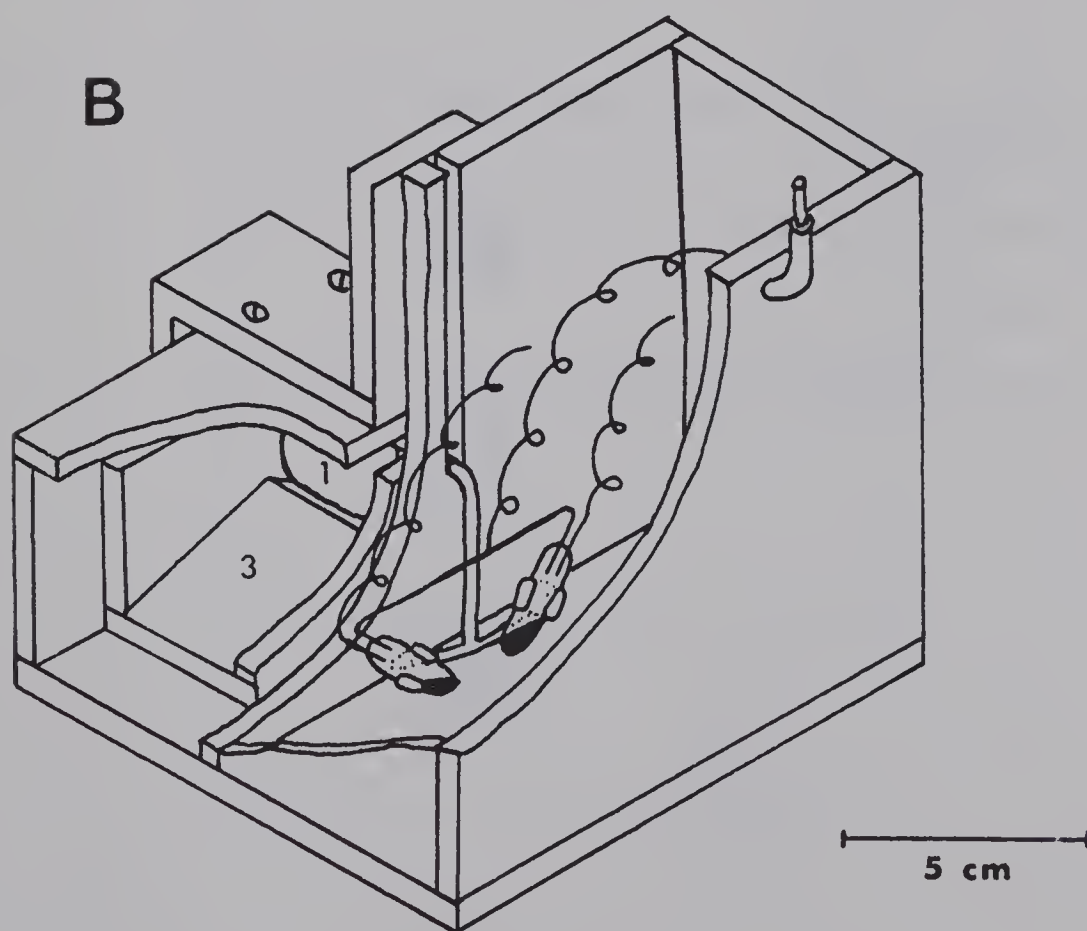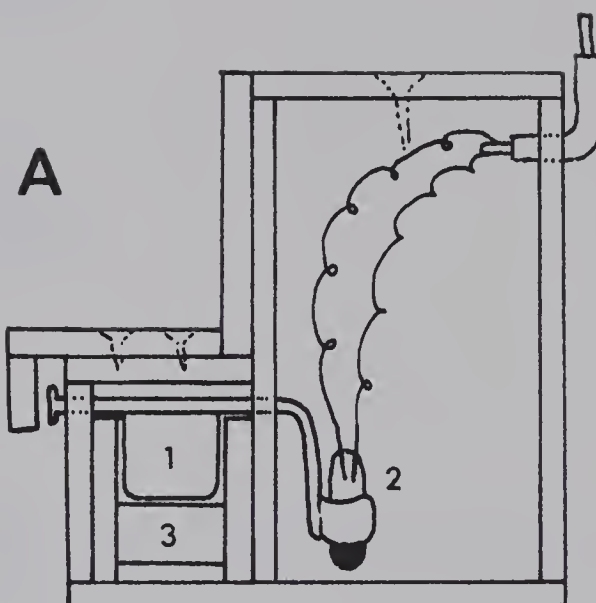
Figure 6. Circuit diagram for first Heart Lake enclosure. Used during the winter of 1970-71 to measure the number of times animals entered passageways to nest boxes, feeders and ports between pens.

MS - Mercury switch (one at each nest box, feeder and port between pens)

CH - Recorder channel

COM - Common

ER - Esterline Angus event recorder
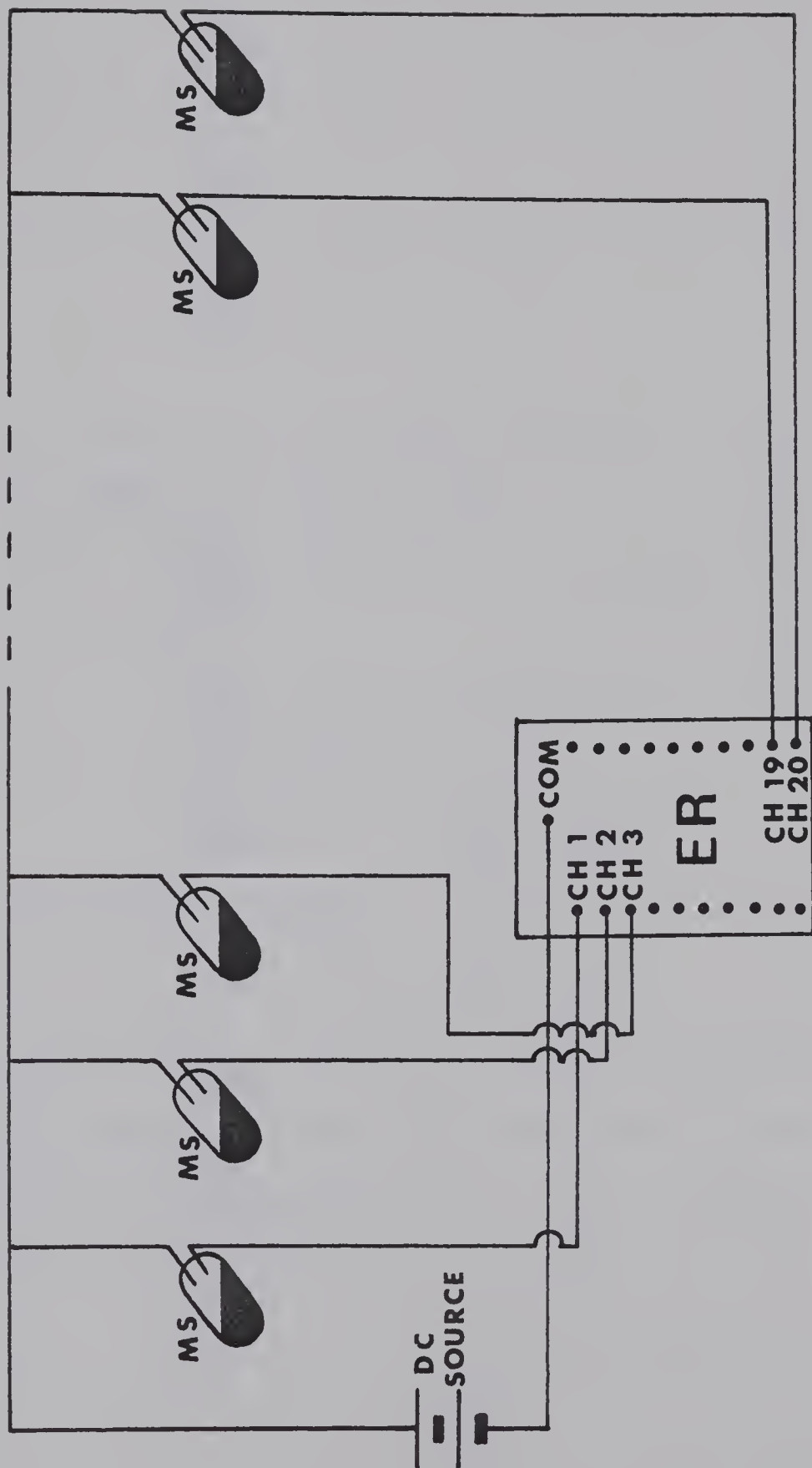
Figure 7.   Circuit diagram for first and second Heart Lake enclosures,

summer of 1971.   Used to measure the number of times animals

used passageways to nest boxes, feeders, and ports between

pens.

MS   - Mercury switch

CH   - Recorder channel

COM - Common

ER   - Esterline Angus event recorder

→►⊢ - Diode

Diodes allow current to pass in one direction only.   Mercury

switch 1 activated only channel 1, mercury switch 2 activated

channels 1 and 2, mercury switch 3 activated only channel 2

and so on.   Thus it was possible to monitor 38 positions with

a 20-channel recorder.
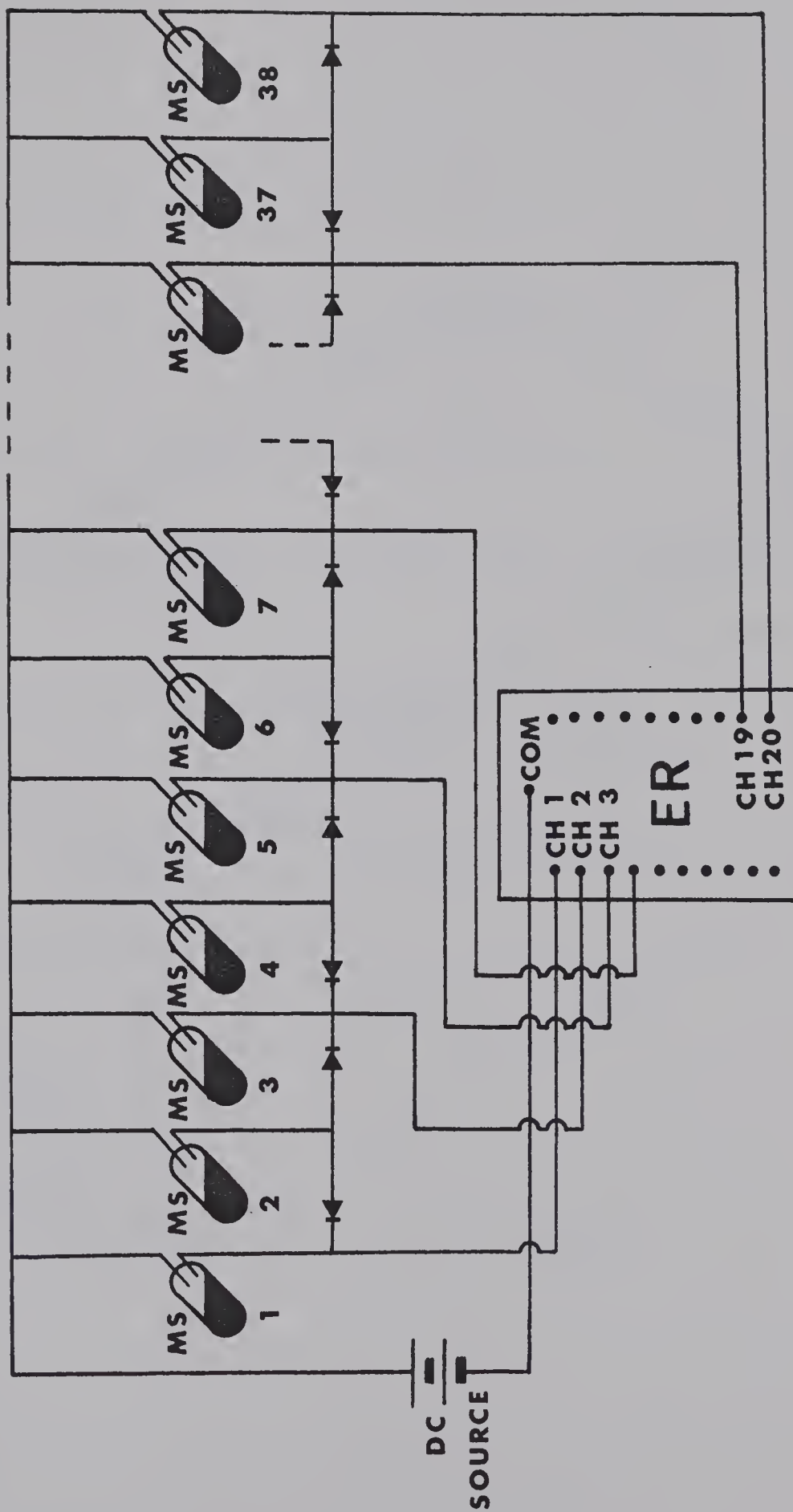
Figure 8.   Arena used to test animals for exploratory behavior and

aggression

       A - Holding box (removable)

       B - Holding box lid

       C - Sliding door to close holding box
           off from arena

15 cm
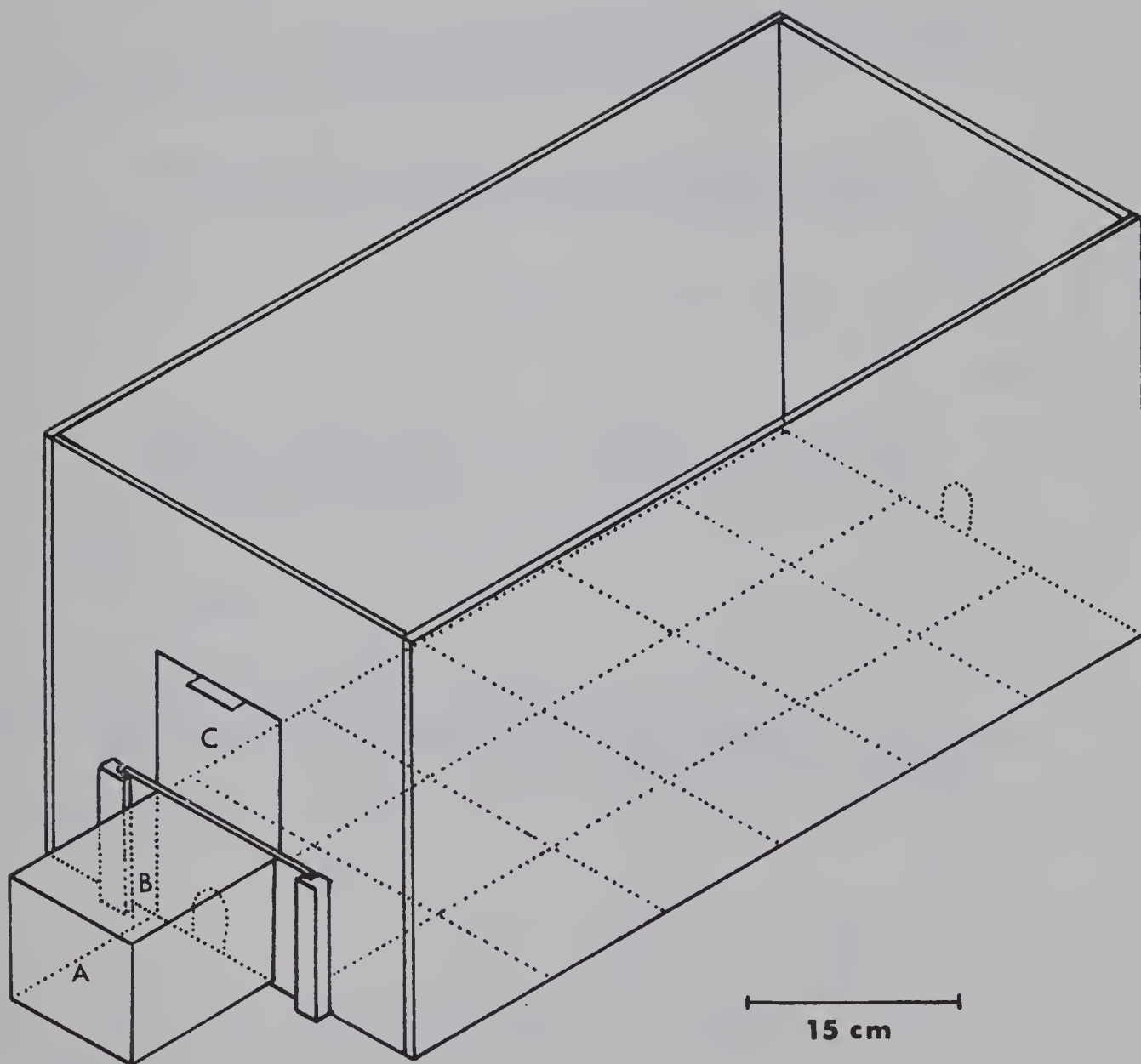
Figure 9. Short-term activity cycle of *C. gapperi* during February 1971

at Lacombe

      ▬▬   Two largest peaks of the day

      ▬   Other activity peaks

    • • •   Sunrise and sunset

    ▓▓▓   Civil twilight (after Berry *et al*. 1945)

Note that larger peaks tend to occur more during daylight and

that peaks occur regularly. Data are given for hourly

intervals preceding the time indicated on the 24 hr clock,

i.e., hour one is the interval from 00:00:01 to 01:00:00.
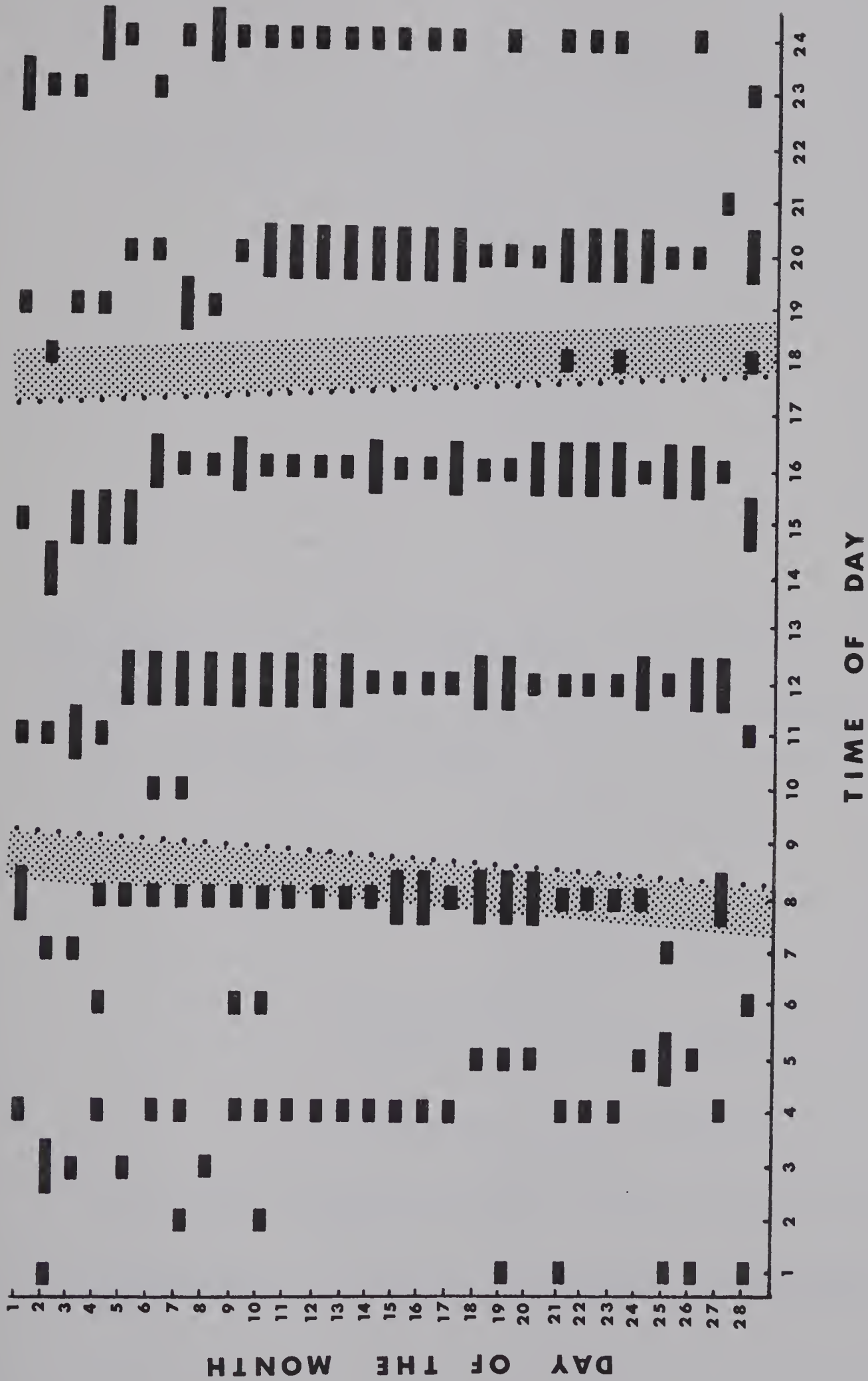
Figure 10. Intervals between peaks of short-term activity cycle of *C. gapperi* during February 1971 at Lacombe. Note that peaks occur nearly every 4 hr (3.80 hr mean interval).

INTERVALS BETWEEN ACTIVITY PEAKS (HR)

FEBRUARY 1971

MEAN { RANGE
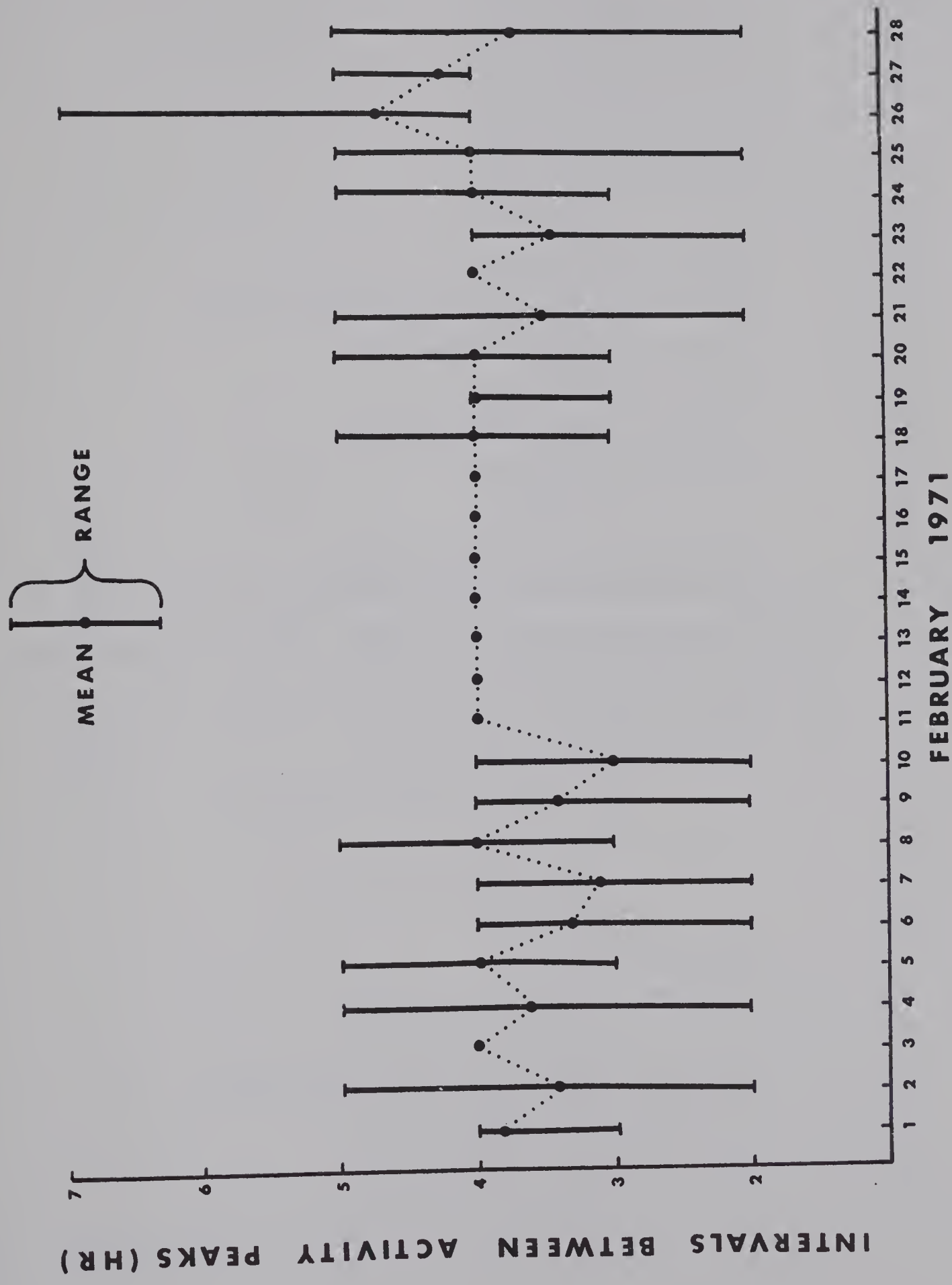
Figure 11.   Intervals between peaks of short-term activity cycle of *C.*
gapperi during July 1971 at Lacombe.   Note that the mean
interval (3.29 hr) is shorter than in winter.
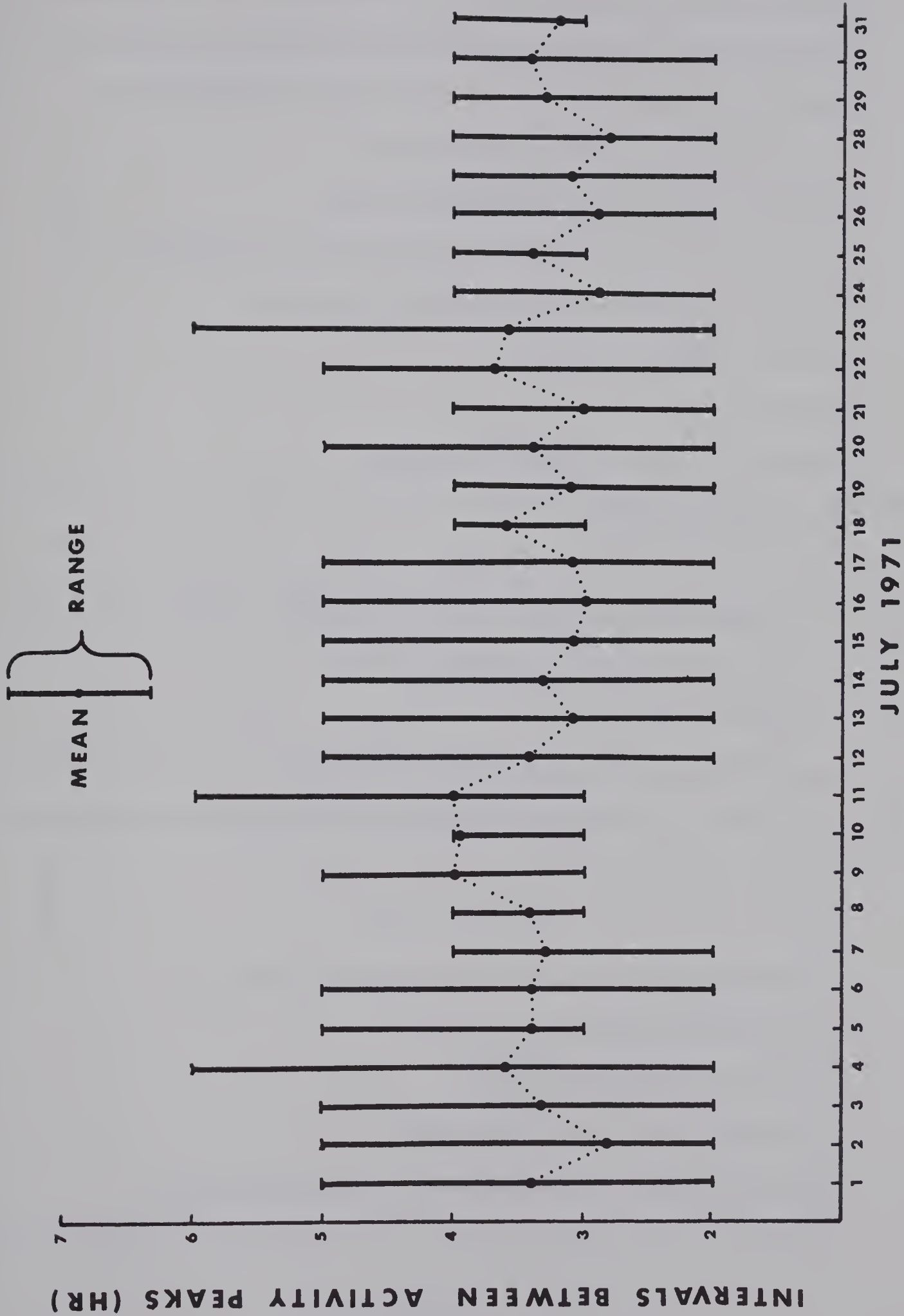
Figure 12.   Example of summer short-term activity cycle of *C. gapperi* at

Lacombe.   Activity was the average daily number of times

animals used passageways to nest boxes, feeders and ports

between pens over the 10-day period from 11 July to 20 July

1971.   Note major peak beginning at 2200 hr and going to

0200 hr.   This 5 hr period has the most sustained activity

of the day.   See Fig. 9 for explanation of the time scale.
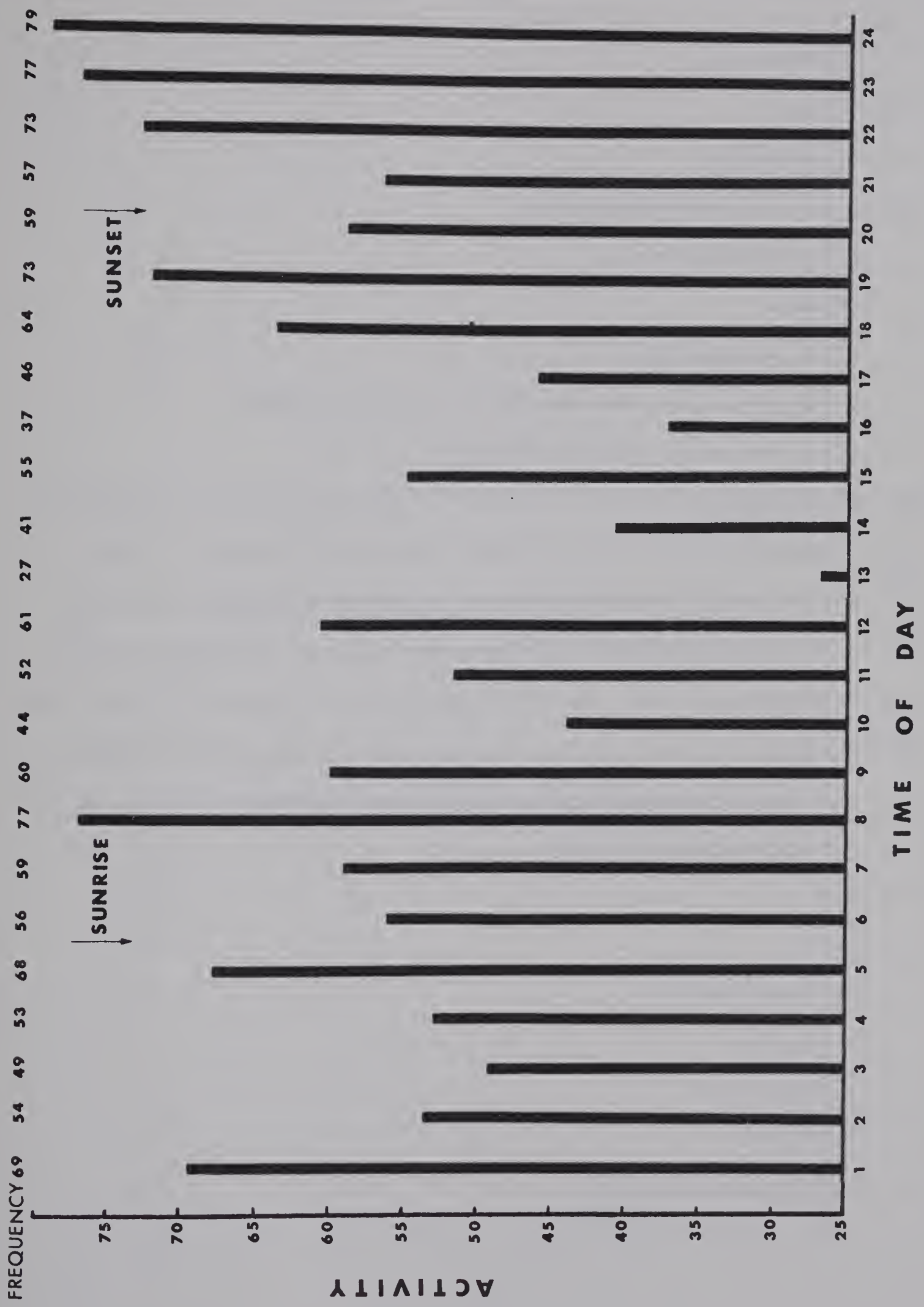
Figure 13. Example of winter short-term activity cycle of *C. gapperi* at
Lacombe. Activity was the average daily number of times
animals used passageways to nest boxes, feeders and ports
between pens over the 9-day period from 21 February to 29
February 1972. Note the higher level of activity during the
day and lower activity at night with no sustained period of
activity comparable to midnight peak in Fig. 12. See Fig. 9
for explanation of time scale.
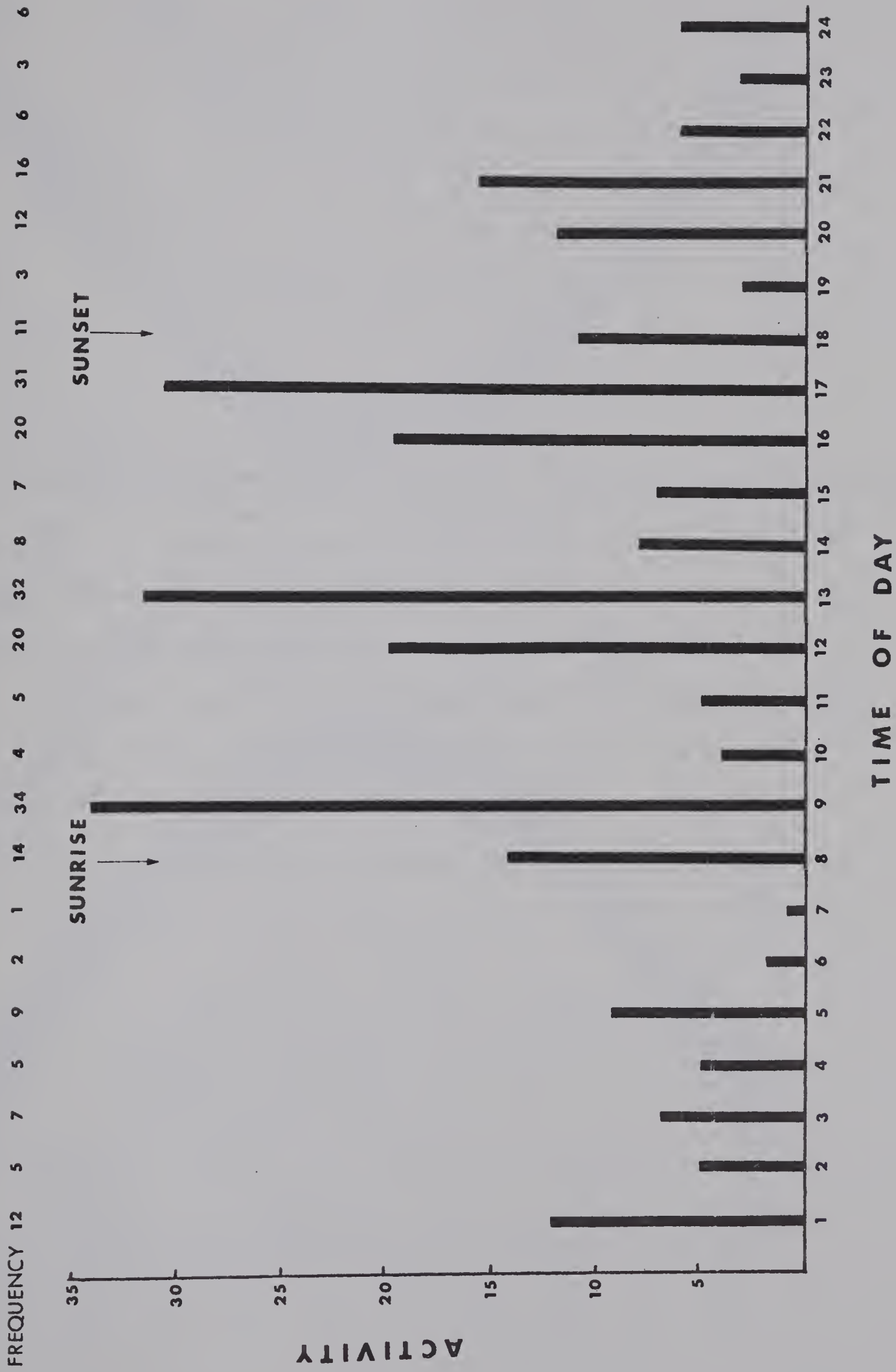
Figure 14.   Frequency of short-term activity peaks of *C. gapperi* during

10-day periods at Heart Lake

■   1-3 peaks per 10-day period

━   4-6 peaks per 10-day period

■━━   7-11 peaks per 10-day period

• • •   Sunrise and sunset

▓▓▓   Civil twilight (after Berry *et al.* 1945)

See Fig. 9 for explanation of time scale.
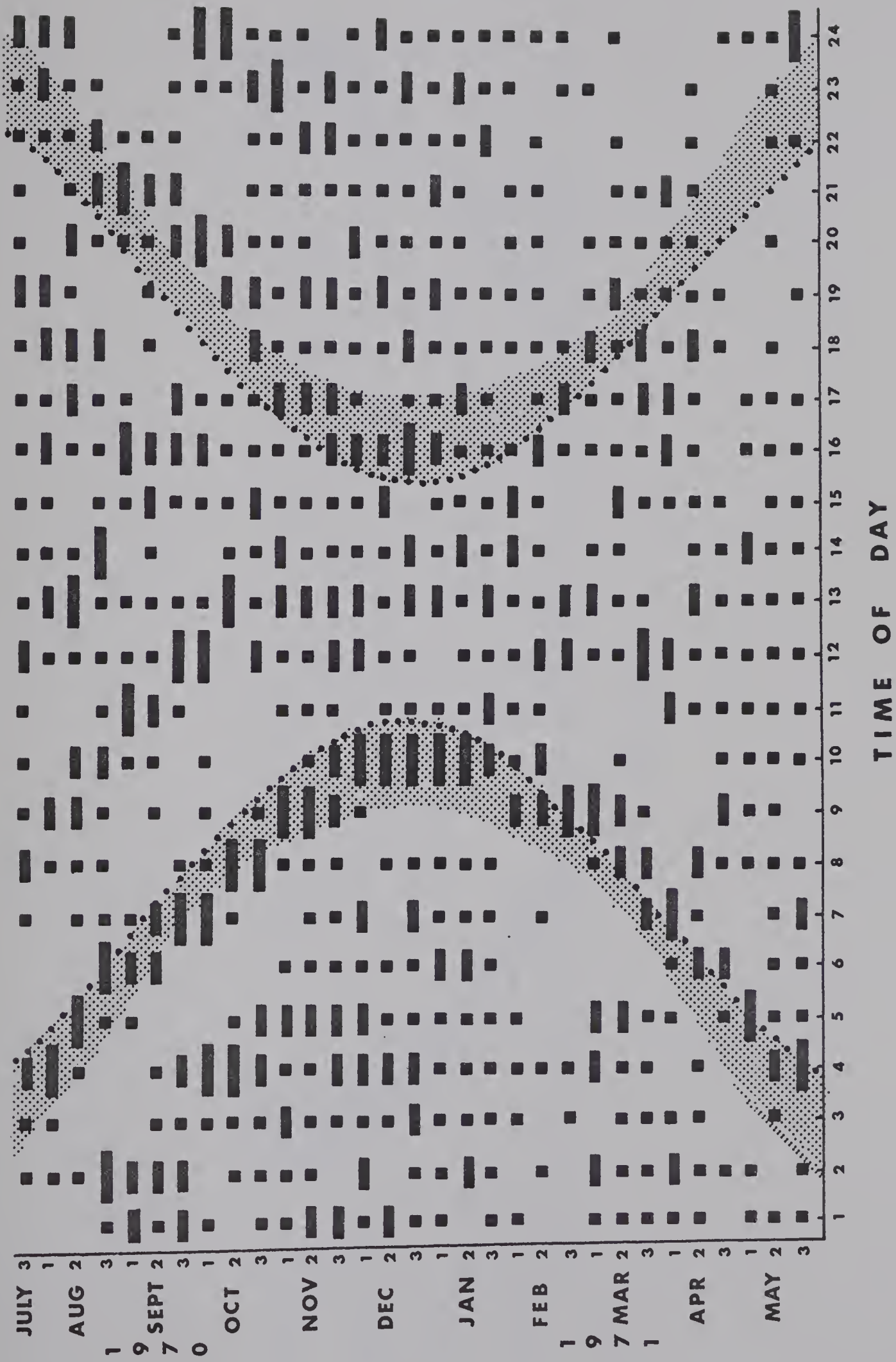
Figure 14. Continued
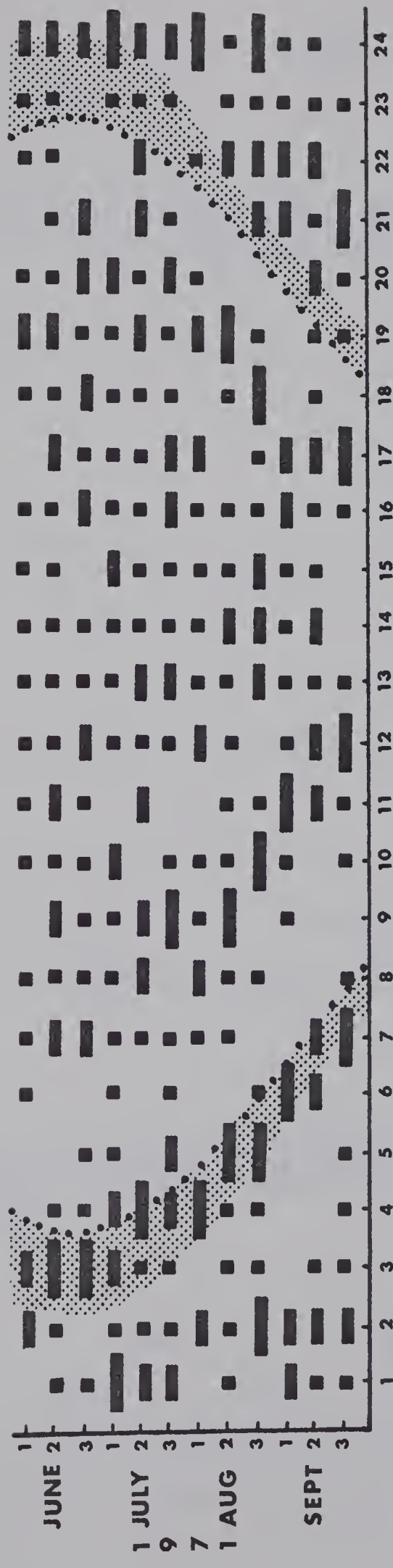
TIME OF DAY

Figure 15. Example of short-term activity cycle of *C. gapperi* during

July 1971 at Lacombe

▰▰ Two largest peaks of the day

▰ Other activity peaks

• • • Sunrise and sunset

▒▒▒ Civil twilight (after Berry *et al*. 1945)

Note that large peaks tend to occur more often during darkness

and with less regularity than in February. See Fig. 9 for

explanation of time scale.

TIME OF DAY

DAY OF THE MONTH
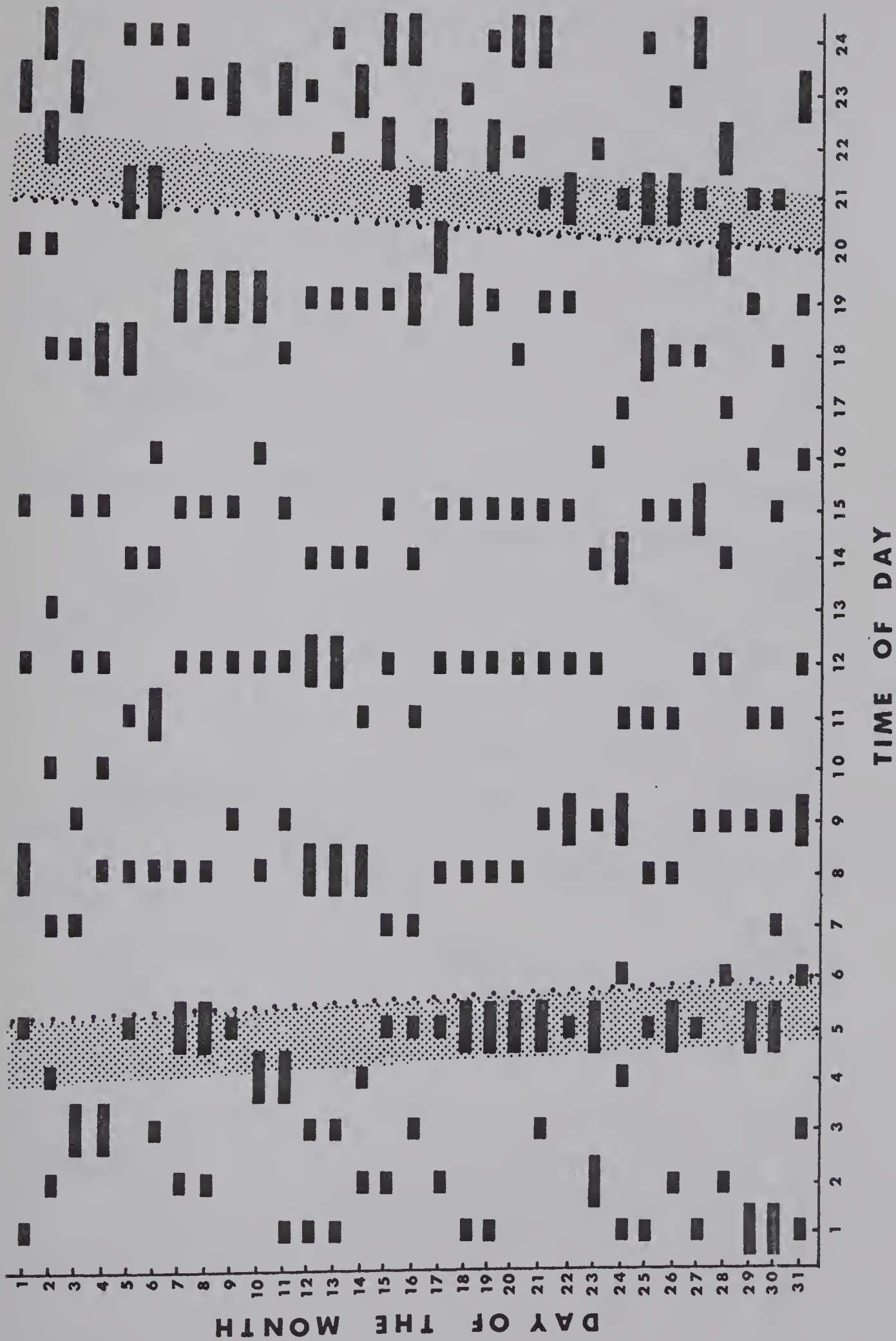
Figure 16. Frequency of short-term activity peaks of *C. gapperi* during

10-day periods at Lacombe

  ■ 1-3 peaks per 10-day period

  ━ 4-6 peaks per 10-day period

  ━━ 7-11 peaks per 10-day period

  • • • Sunrise and sunset

  ▦ Civil twilight (after Berry *et al.* 1945)

See Fig. 9 for explanation of time scale.
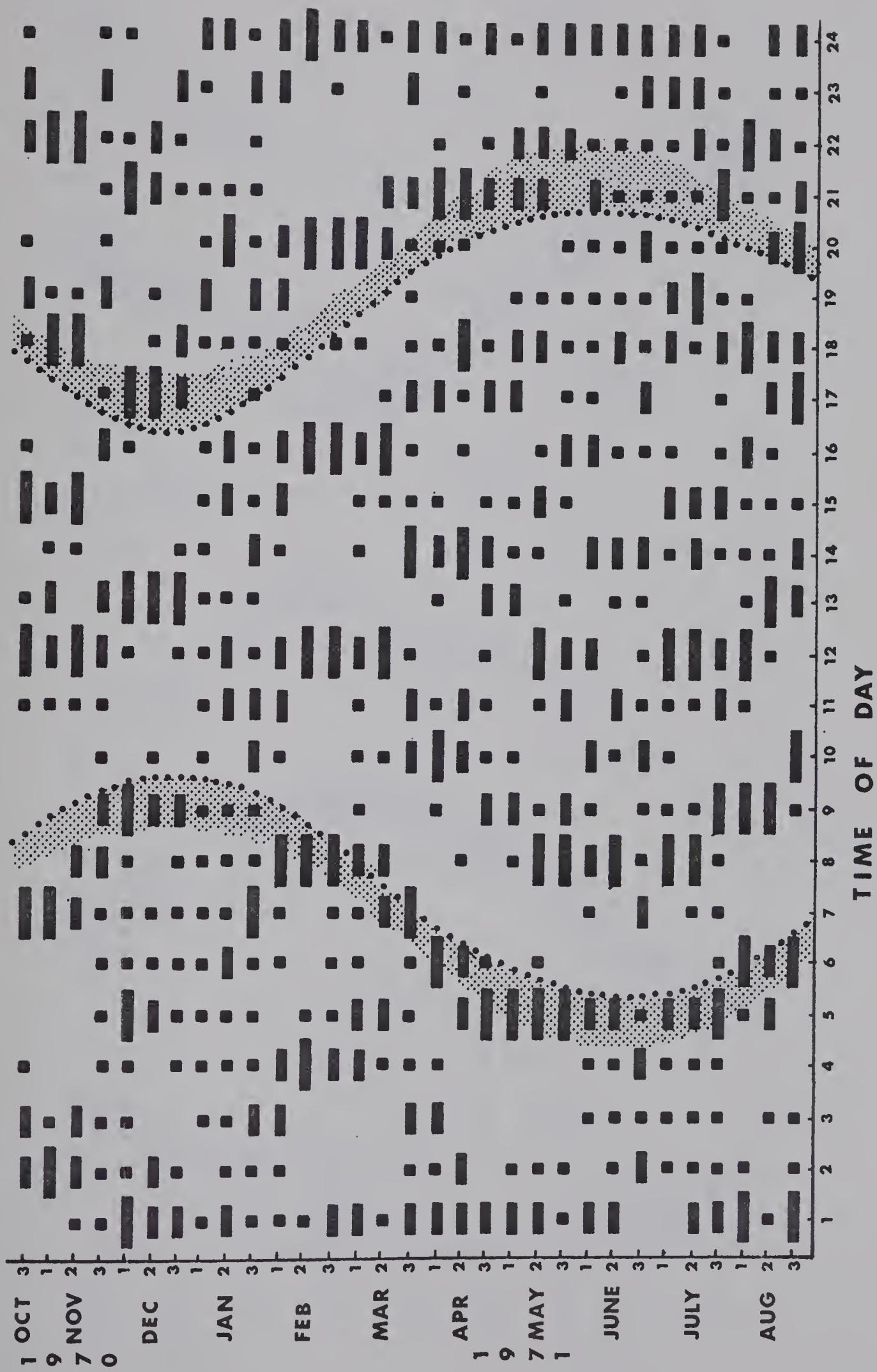
Figure 16. Continued
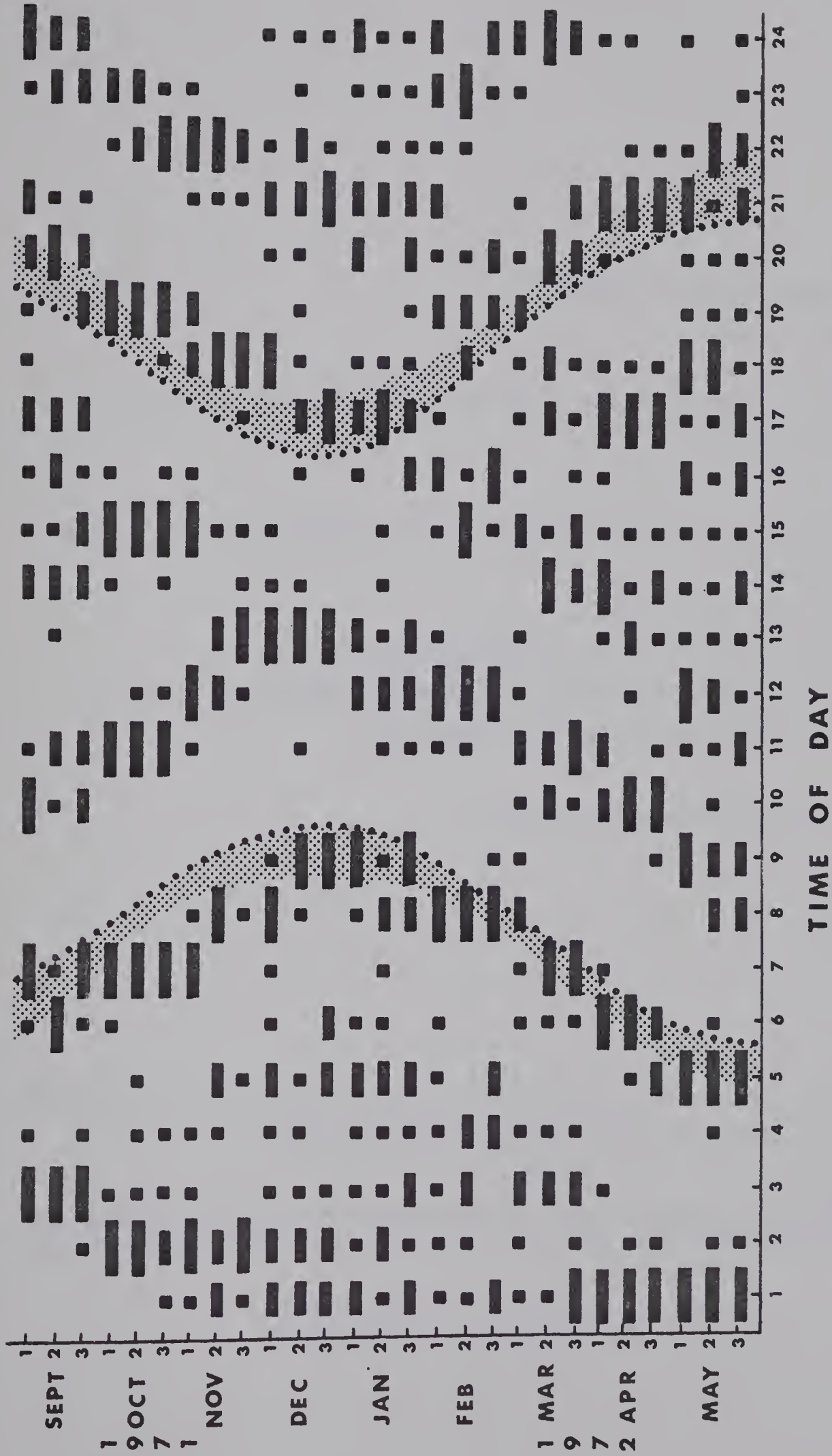
Figure 17. Daily hours of sunshine at Lacombe, January 1971.

HOURS OF SUNSHINE

JANUARY 1971
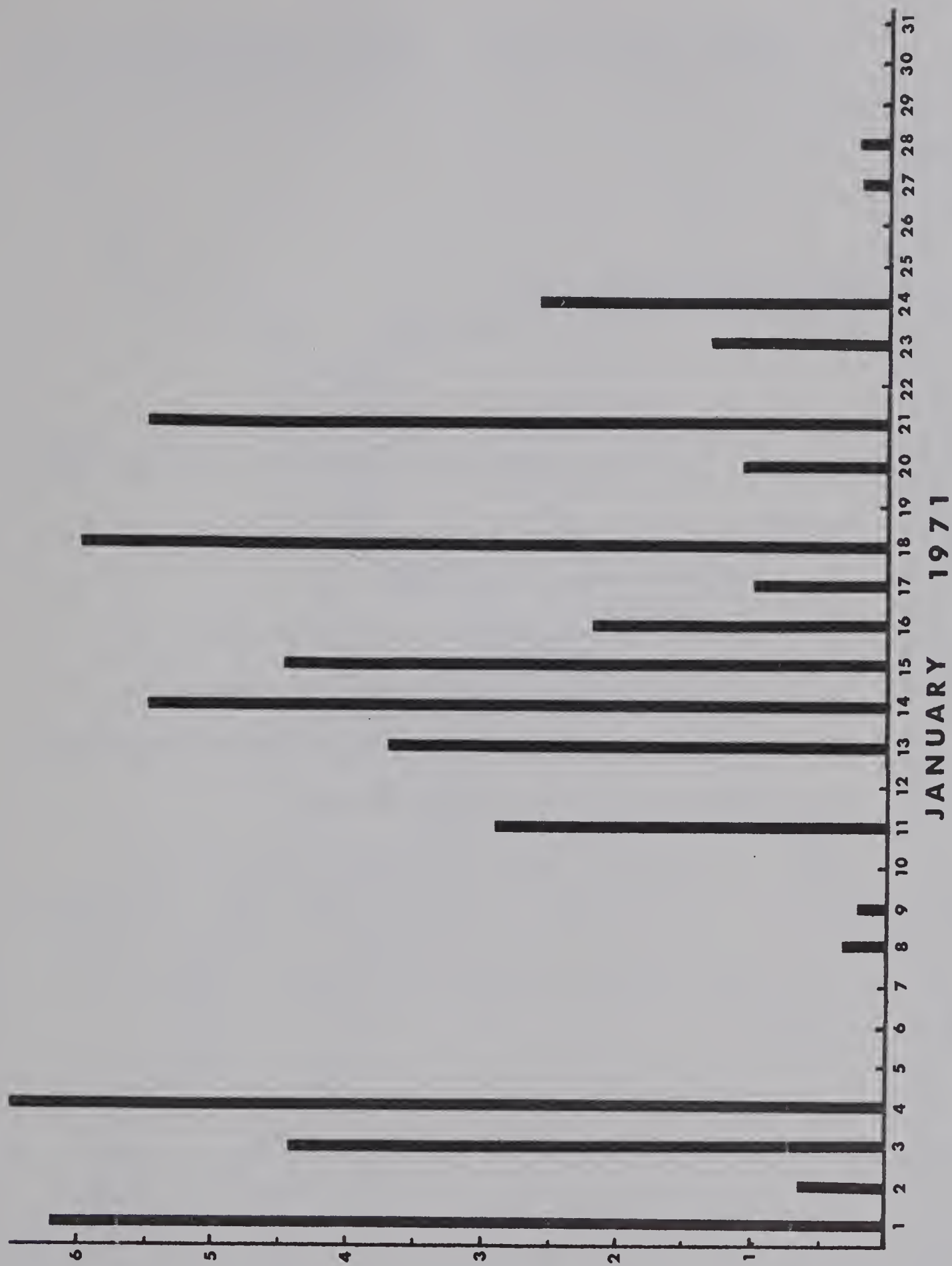
Figure 18. Activity, temperature and snow at Heart Lake, August 1970 to May 1971

1   Marten tracks in enclosure

2 - 6   Weasel tracks observed in the enclosure

●   10-day average of daily mean air temperature

▲   10-day average of daily mean subnivean temperature

■   Total activity in the enclosure

━   Average snow depth during each 10-day period

Activity was the number of times animals used passageways to nest boxes, feeders and ports between pens during 10-day periods.
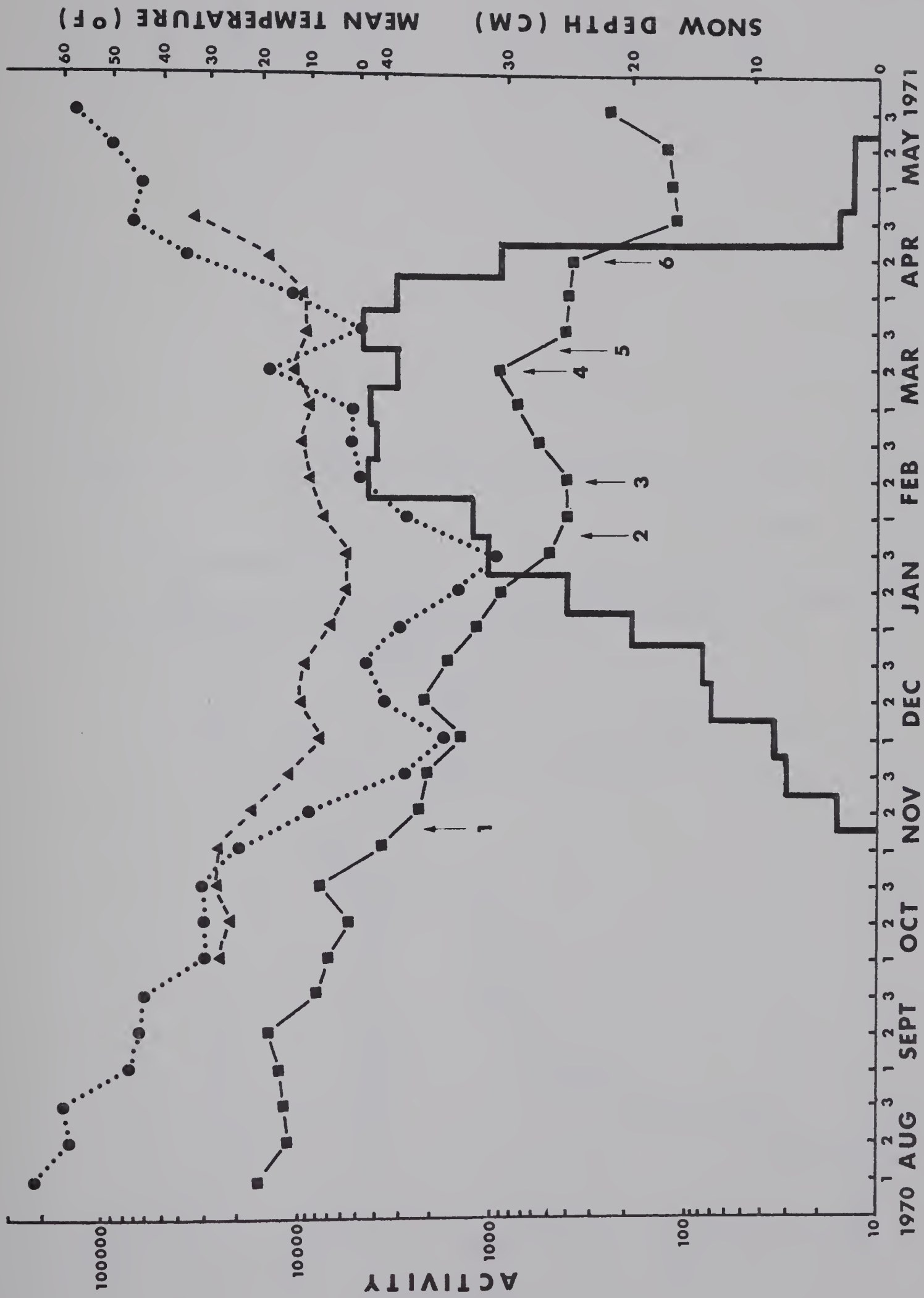
Figure 19. Activity, temperature and snow at Lacombe, October 1970 to

August 1971

●   10-day average of daily mean air temperature

▲   10-day average of daily mean subnivean temperature

■   Total activity in the enclosure

━━   Average snow depth during each 10-day period

See Fig. 18 for explanation of activity.
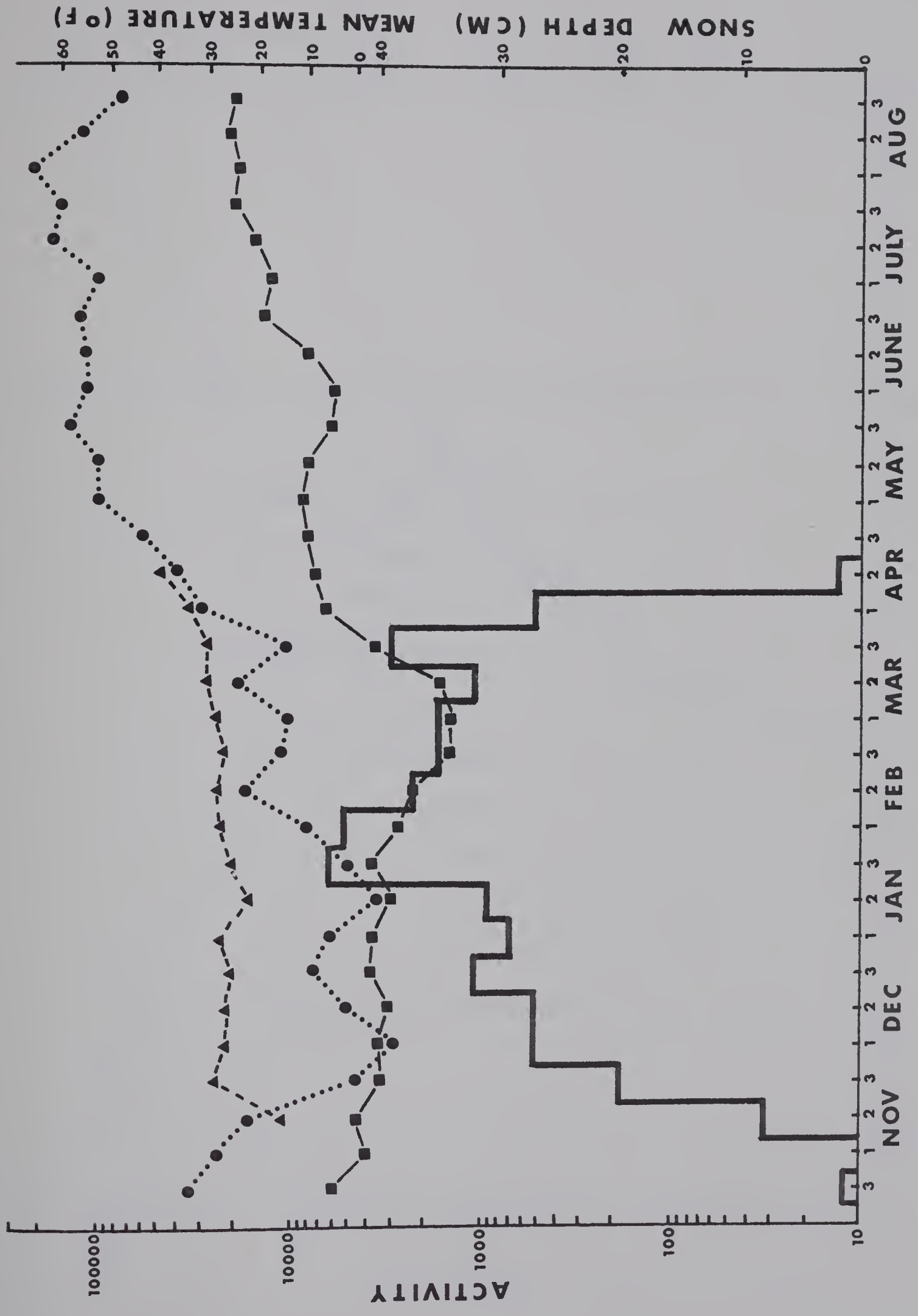
Figure 20. Activity, temperature and snow at Lacombe, August 1971 to May

1972

●   10-day average of daily mean air temperature

▲   10-day average of daily mean subnivean temperature

■   Total activity in the enclosure

━   Average snow depth during each 10-day period

1   - Population was 21 animals

2   - Population was 12 animals

3   - Population was 9 animals

4   - Population was 8 animals

5   - Population was 7 animals

6   - Population was 7 animals

See Fig. 18 for explanation of activity.
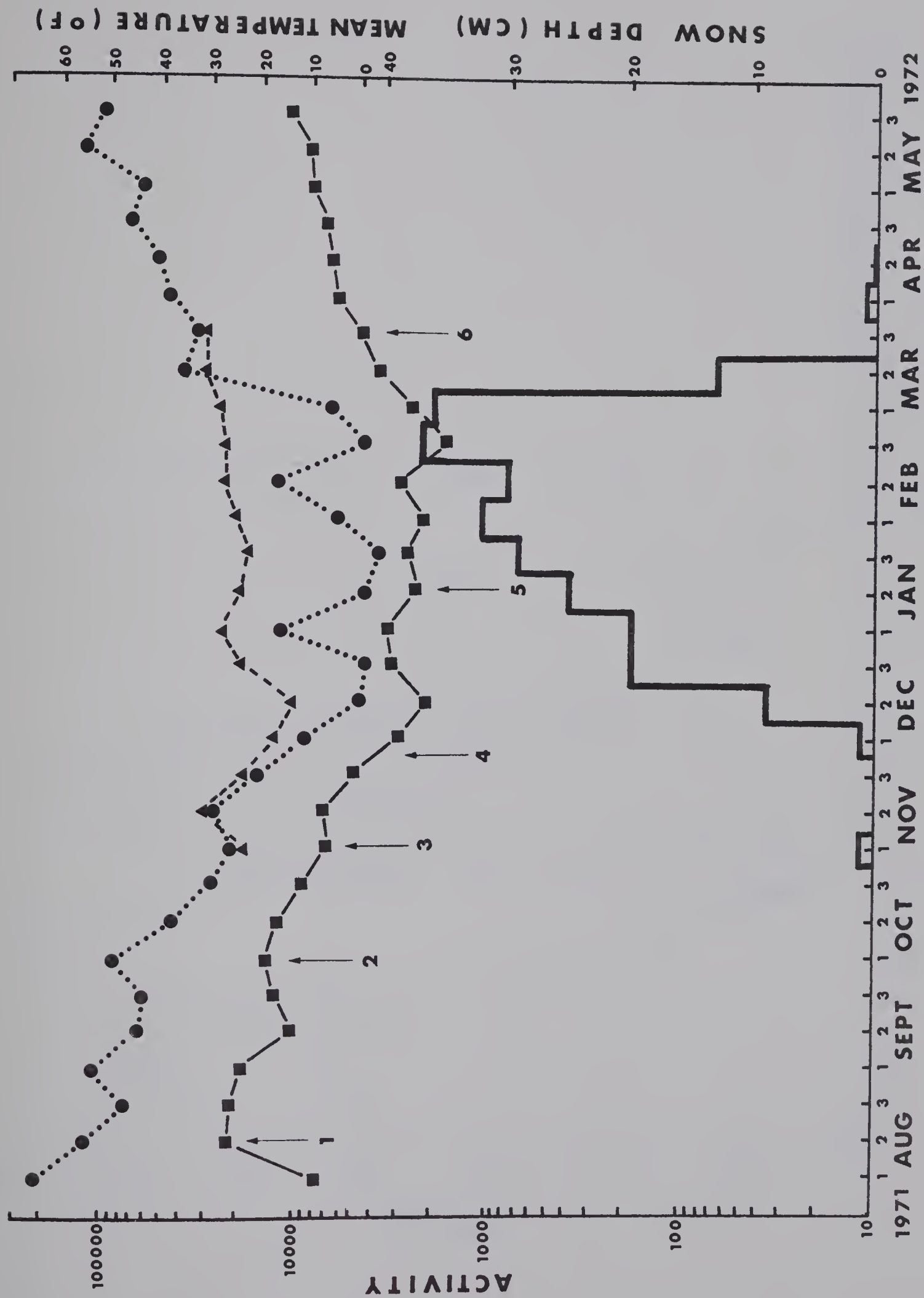
Figure 21. Use of nest boxes by *C. gapperi* at Heart Lake during the

winter of 1970-71

● Nest boxes in pens A and D

○ Nest boxes in pens B and E

△ Nest boxes in pens C and F

⟶ Weasel and marten tracks observed in enclosure

Activity was the number of times animals used passageways to

nest boxes during 10-day periods. Note that the number of

animals in the enclosure was probably decreasing.
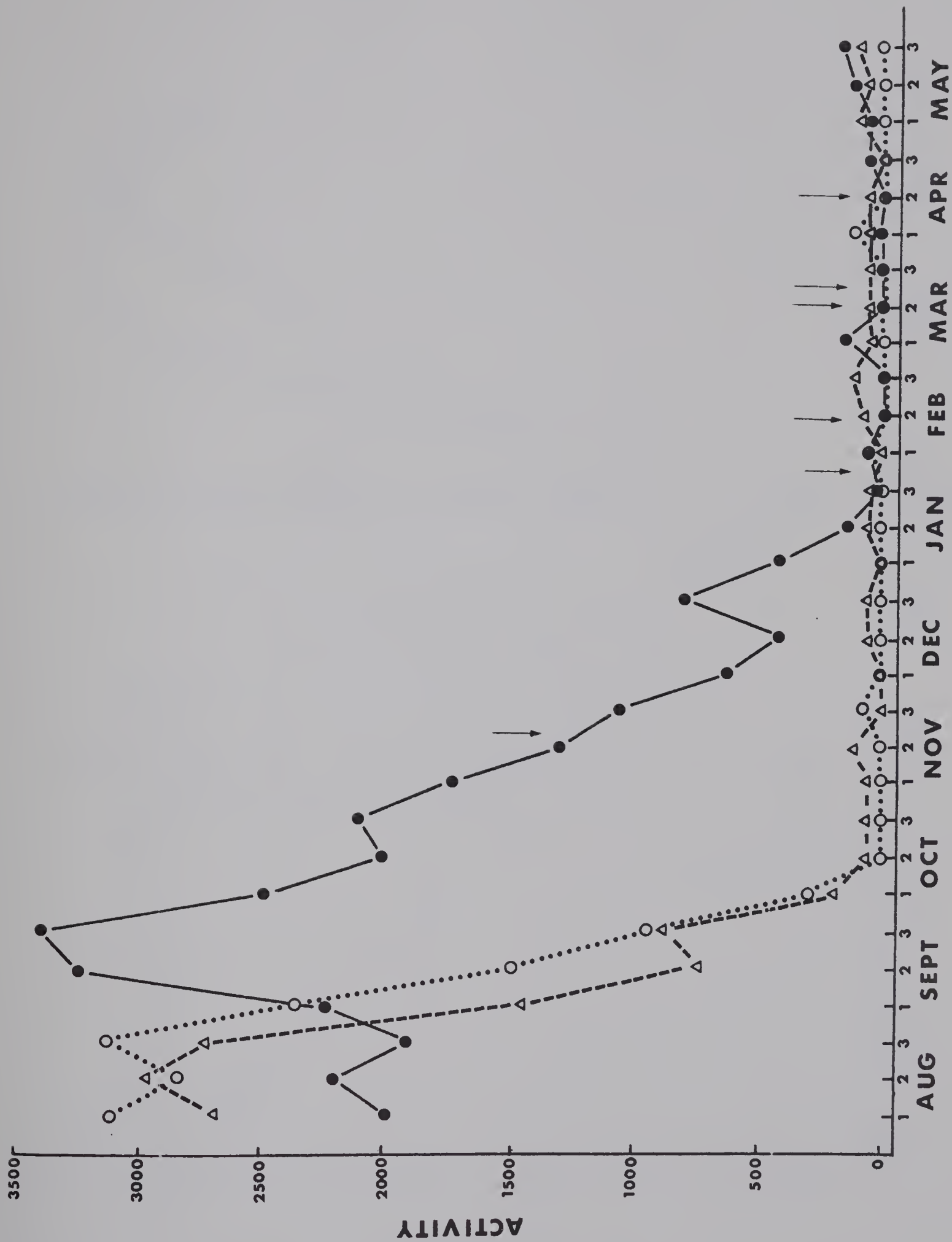
Figure 22. Use of nest boxes by *C. gapperi* at Lacombe during the winter

of 1970-71

□   Nest boxes in pen A

△   Nest boxes in pen B

O   Nest boxes in pen C

See Fig. 21 for explanation of activity. Note that declines

in pens B and C and increases in all pens appear to be

exponential.
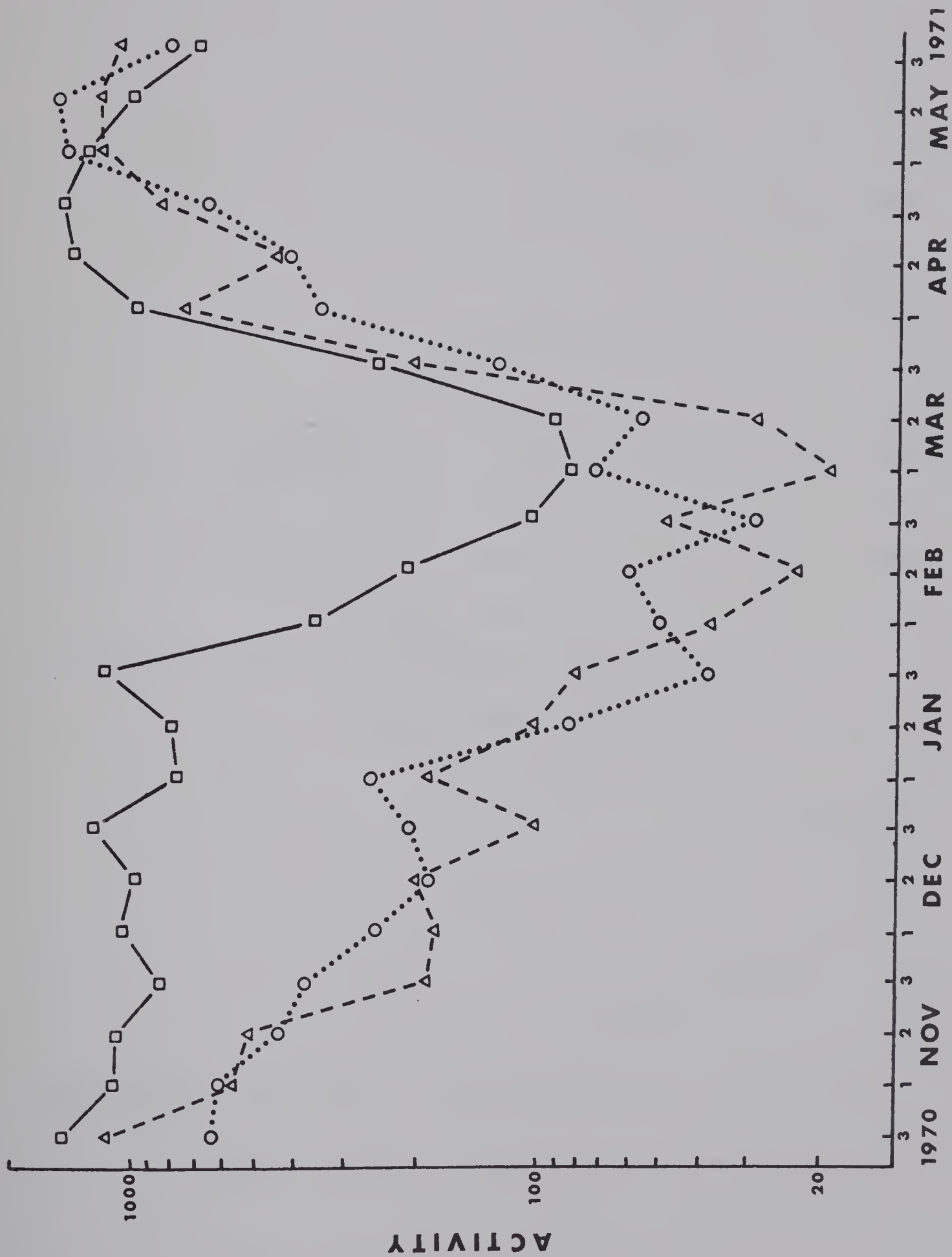
Figure 23. Use of feeders by *C. gapperi* during monthly periods at Lacombe

□   Feeder in pen A

△   Feeder in pen B

○   Feeder in pen C

Activity was the number of times animals used passageways to each feeder during the month.
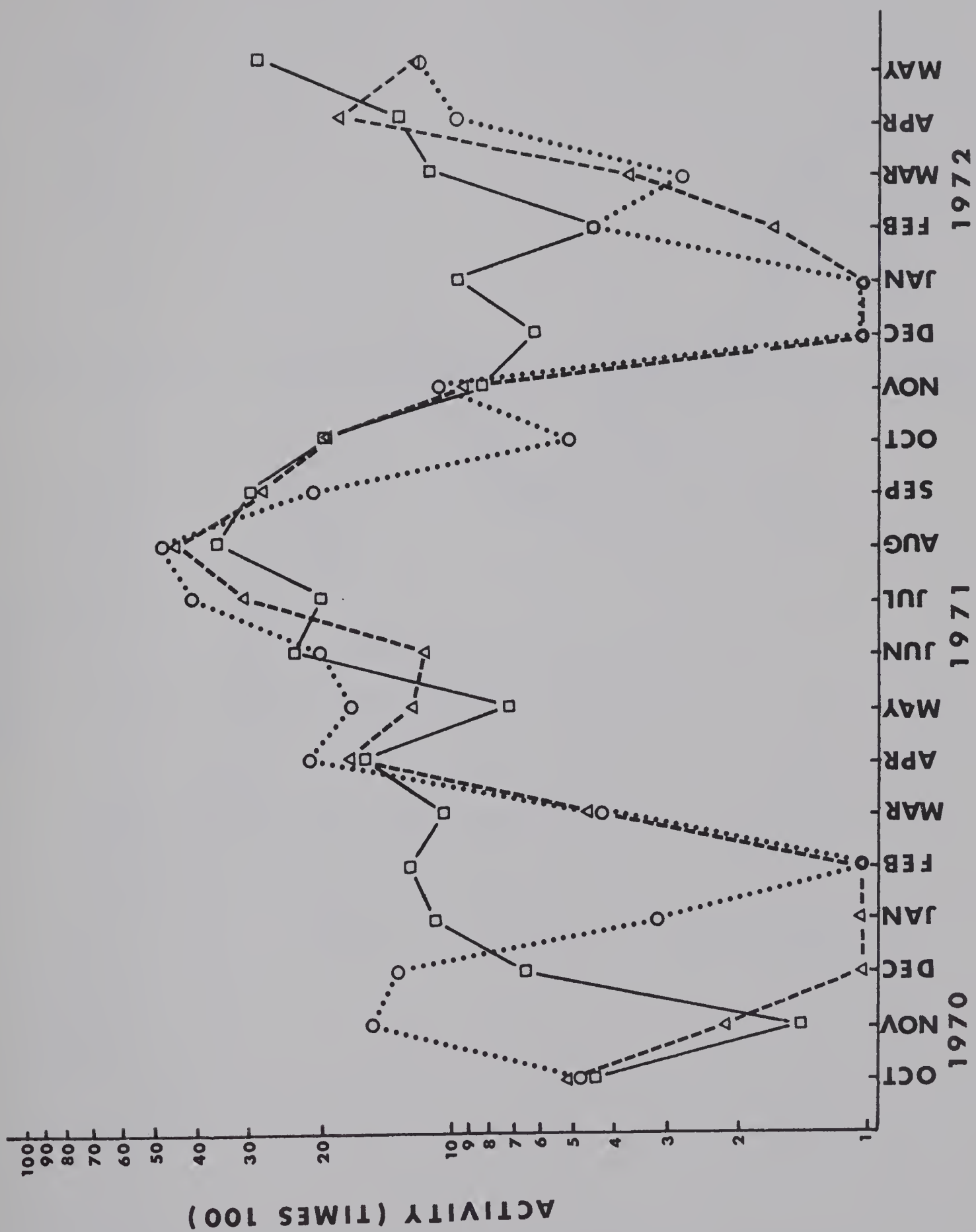
Figure 24. Use of nest boxes by *C. gapperi* in each pen at Lacombe during

the summer of 1971

□ Nest boxes in pen A

△ Nest boxes in pen B

○ Nest boxes in pen C

1 - First litter born in pen A to No. 31

2 - Second litter born in pen A to No. 31

3 - Third litter born in pen A to No. 31

4 - Fourth and fifth litters born (eaten within 24 hr)

5 - Sixth litter born (eaten within 24 hr)

See Fig. 21 for explanation of activity.
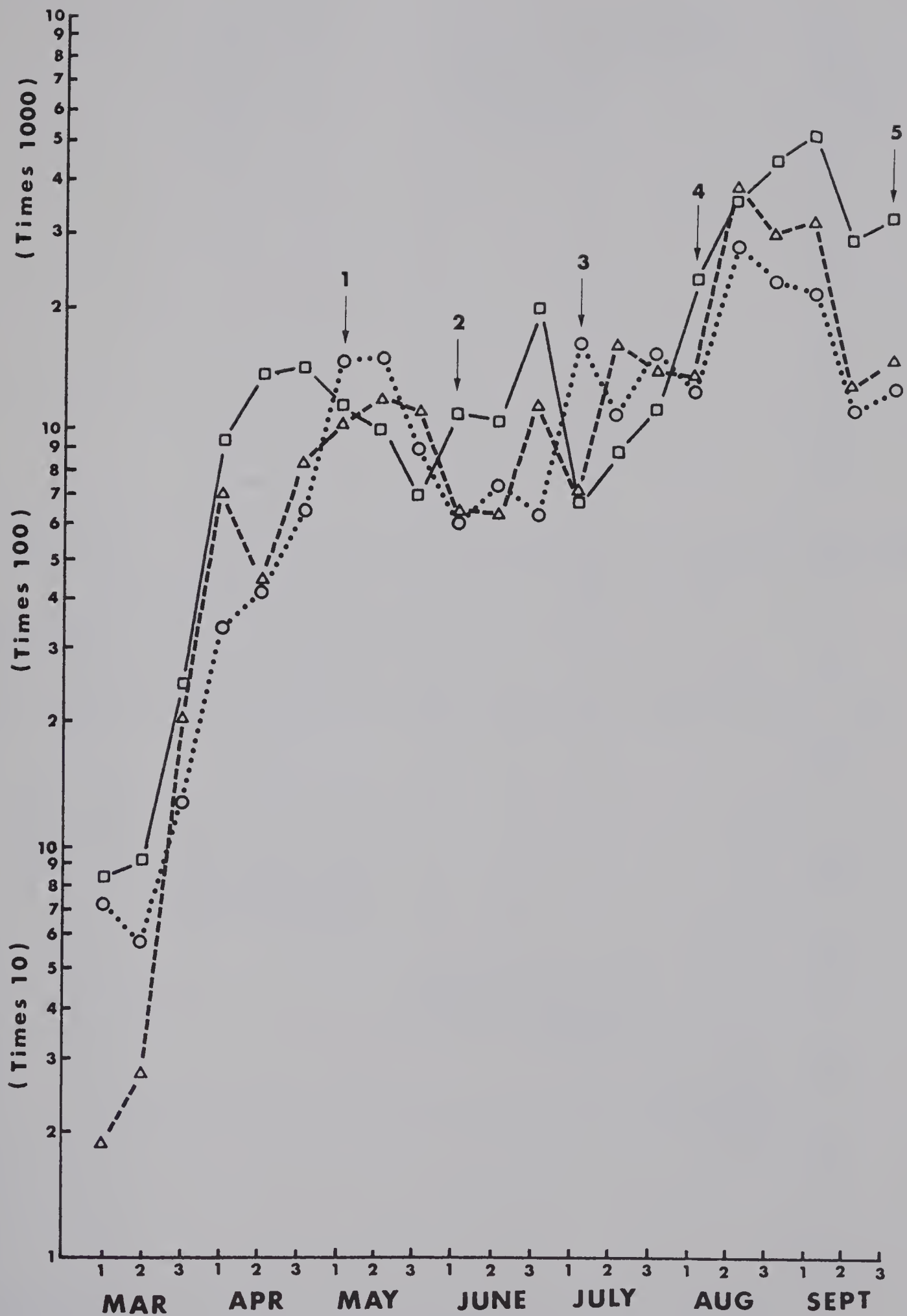
Figure 25. Population mortality and natality at Lacombe. Lines begin

at birth or capture and end at death. Dotted line

indicates approximate time of death. Enclosure stocked with

six animals caught at Heart Lake in the fall of 1970.
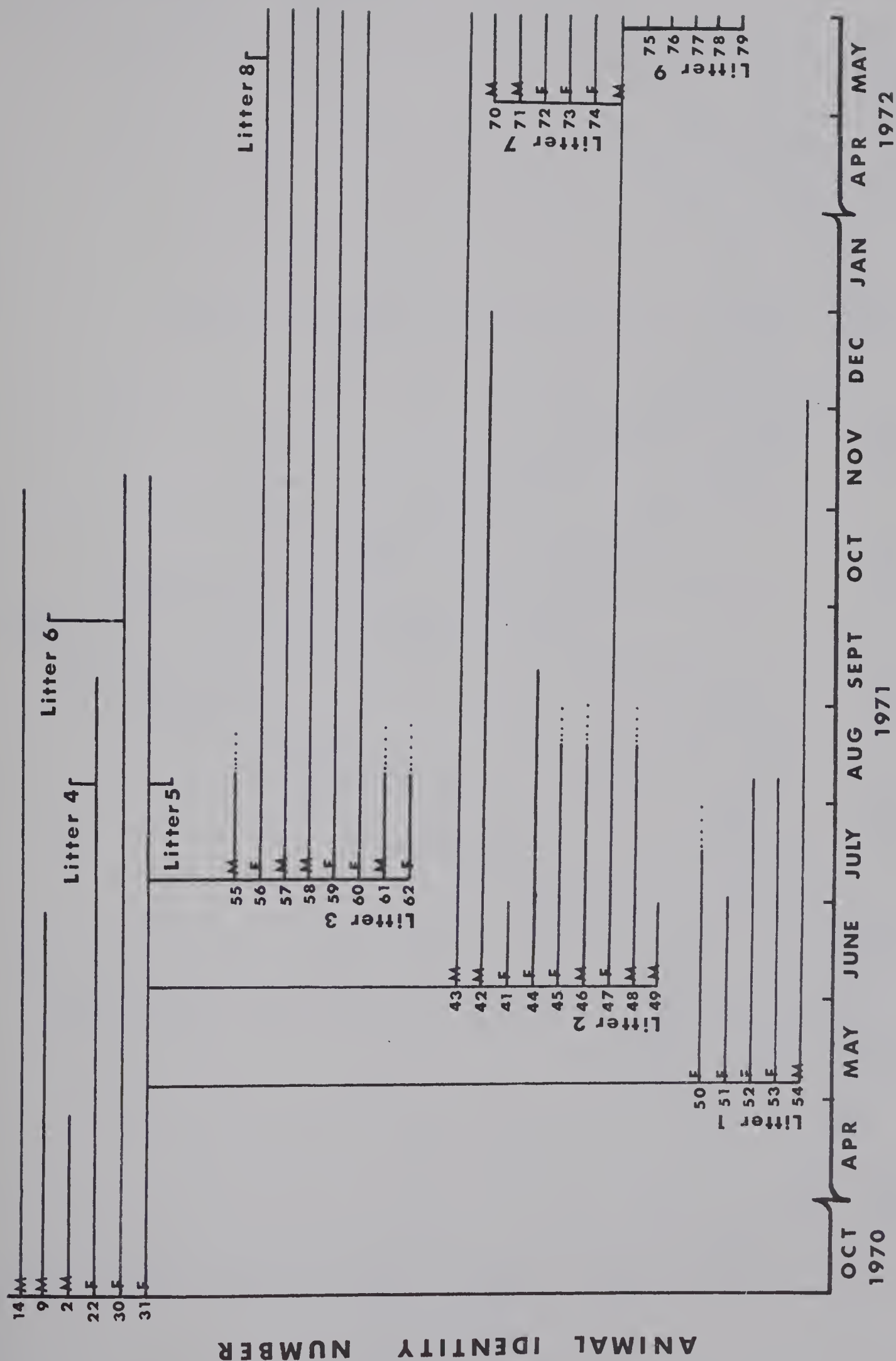
Figure 26. Average monthly activity of *C. gapperi* at Lacombe

◻ Nest boxes in pen A

○ Nest boxes in pen B

△ Nest boxes in pen C

▼ Activity in feeders

● Movements between pens

■ Number of weaned animals in the enclosure

1 – First litter born

2 – Second litter born

3 – Third litter born

4 – Fourth and fifth litters born

5 – Sixth litter born

Activity was the daily average number of times animals used passageways to nest boxes, feeders or ports between pens during each month.
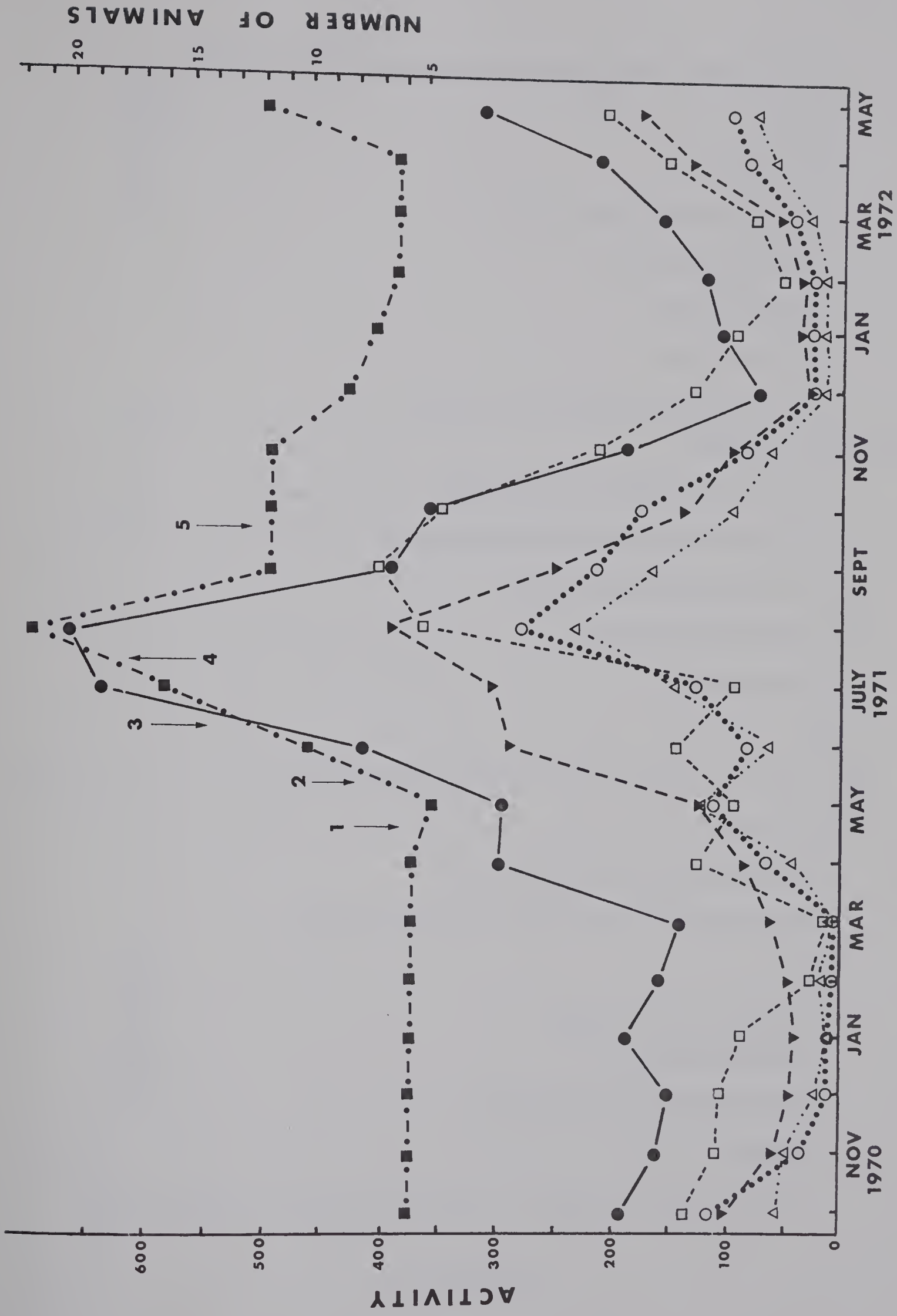
Figure 27. Examples of daily short-term activity cycles in summer.

A - *C. gapperi* in second Heart Lake enclosure, 19 June 1971

B - *C. rutilus* in second Heart Lake enclosure, 19 June 1971

C - *P. maniculatus* in first Heart Lake enclosure, 6 June 1971

Note that the activity pattern of *P. maniculatus* is bimodal, nocturnal. *C. rutilus* activity is lower than *C. gapperi* during the same period. See Fig. 9 for explanation of time scale. Activity was the number of times animals used passageways to nest boxes, feeders and ports between pens each day.
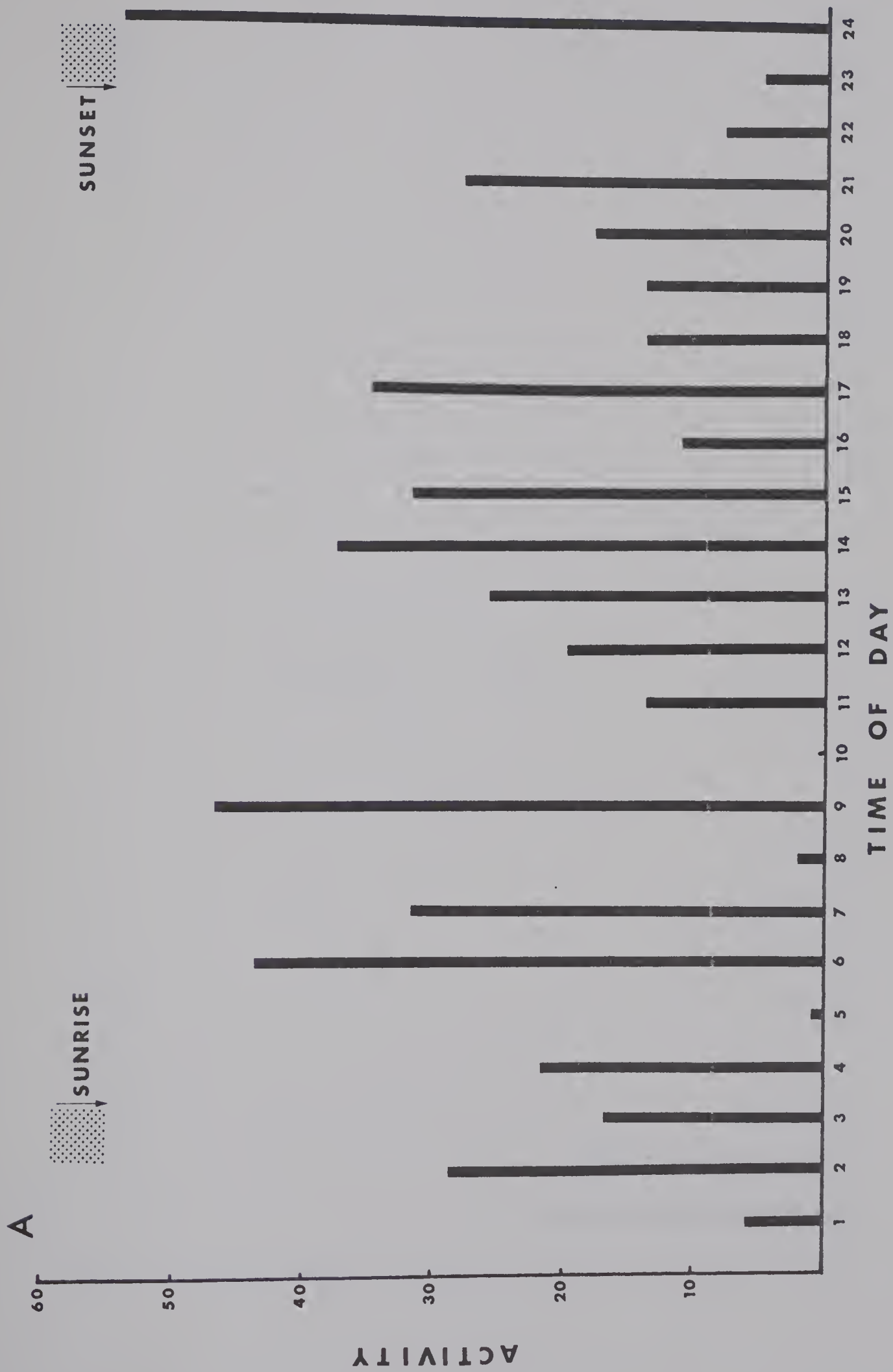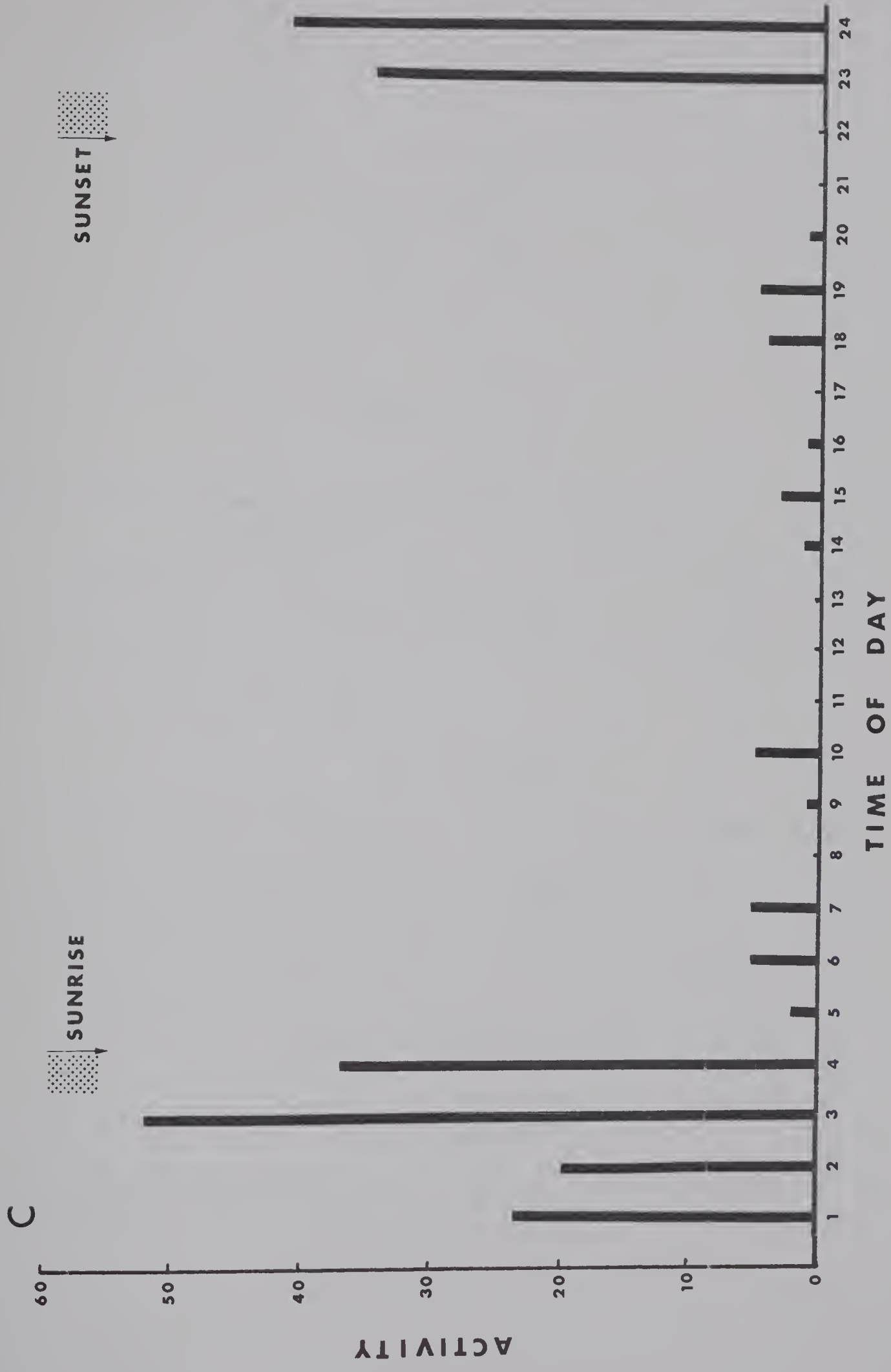
A

Figure 27. Continued

Figure 27. Continued

Figure 28. Interactions of *P. maniculatus* and *C. gapperi* adults in pens

A and D of first Heart Lake enclosure

□   Nest boxes in pen A

△   Feeder in pen A

■   Nest boxes in pen D

▲   Feeder in pen D

Prior to 27 June only *C. gapperi* were in pen A and only

P. maniculatus were in pen D. After the port between units

was opened both species had access to each side. Activity

was the number of times animals used the passageways to nest
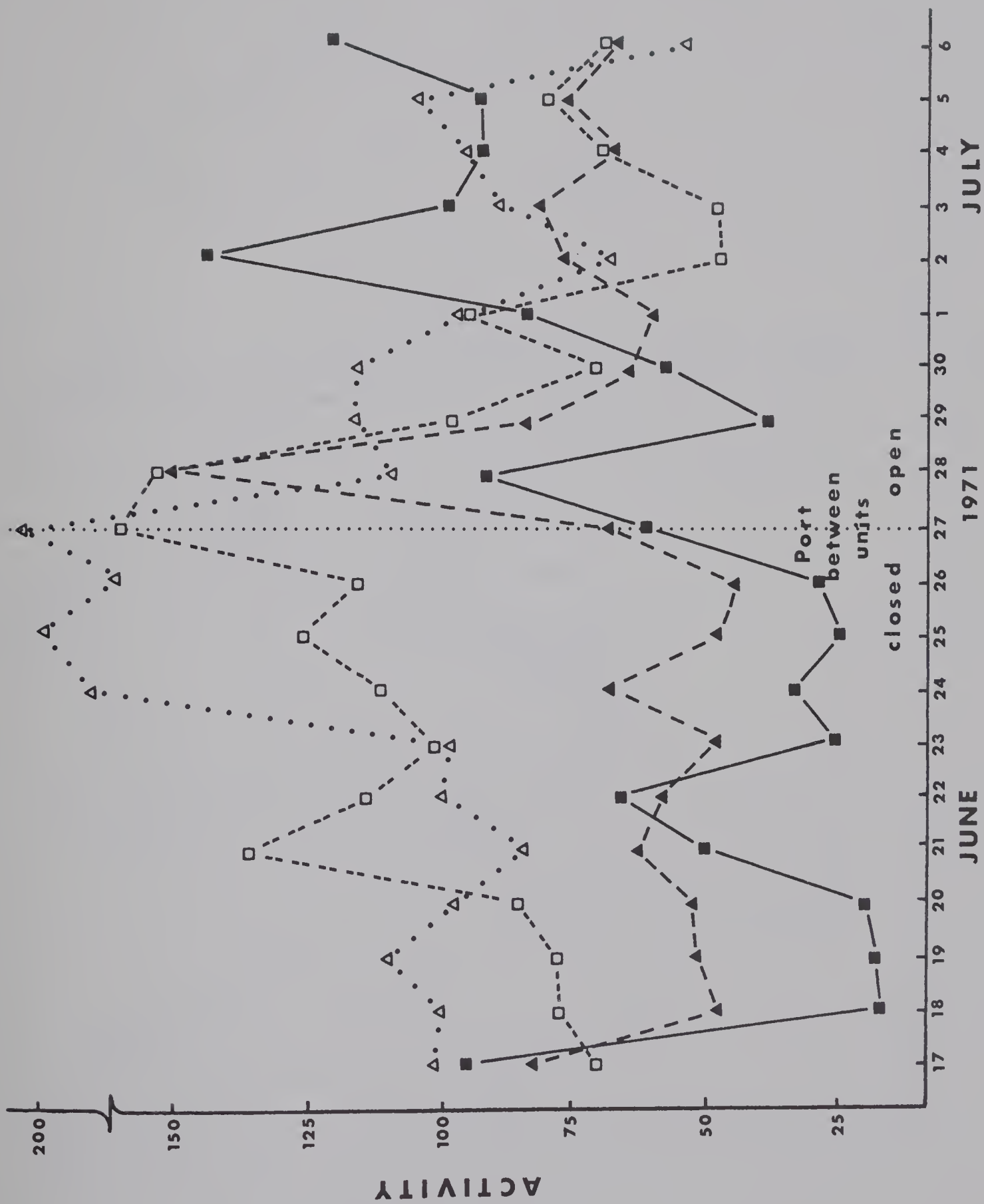
boxes or feeders during each day.

Figure 29. Example of interactions between *C. gapperi* and *C. rutilus* in pens A and D of second Heart Lake enclosure. Two adults and two sub-adults of each species were present.

           □   Nest boxes in pen A

           △   Feeders in pen A

           ■   Nest boxes in pen D

           ▲   Feeders in pen D

Prior to 15 August only *C. gapperi* were in pen A and only *C. rutilus* were in pen D. After the port joining units was opened both species had access to each side. See Fig. 28 for explanation of activity.
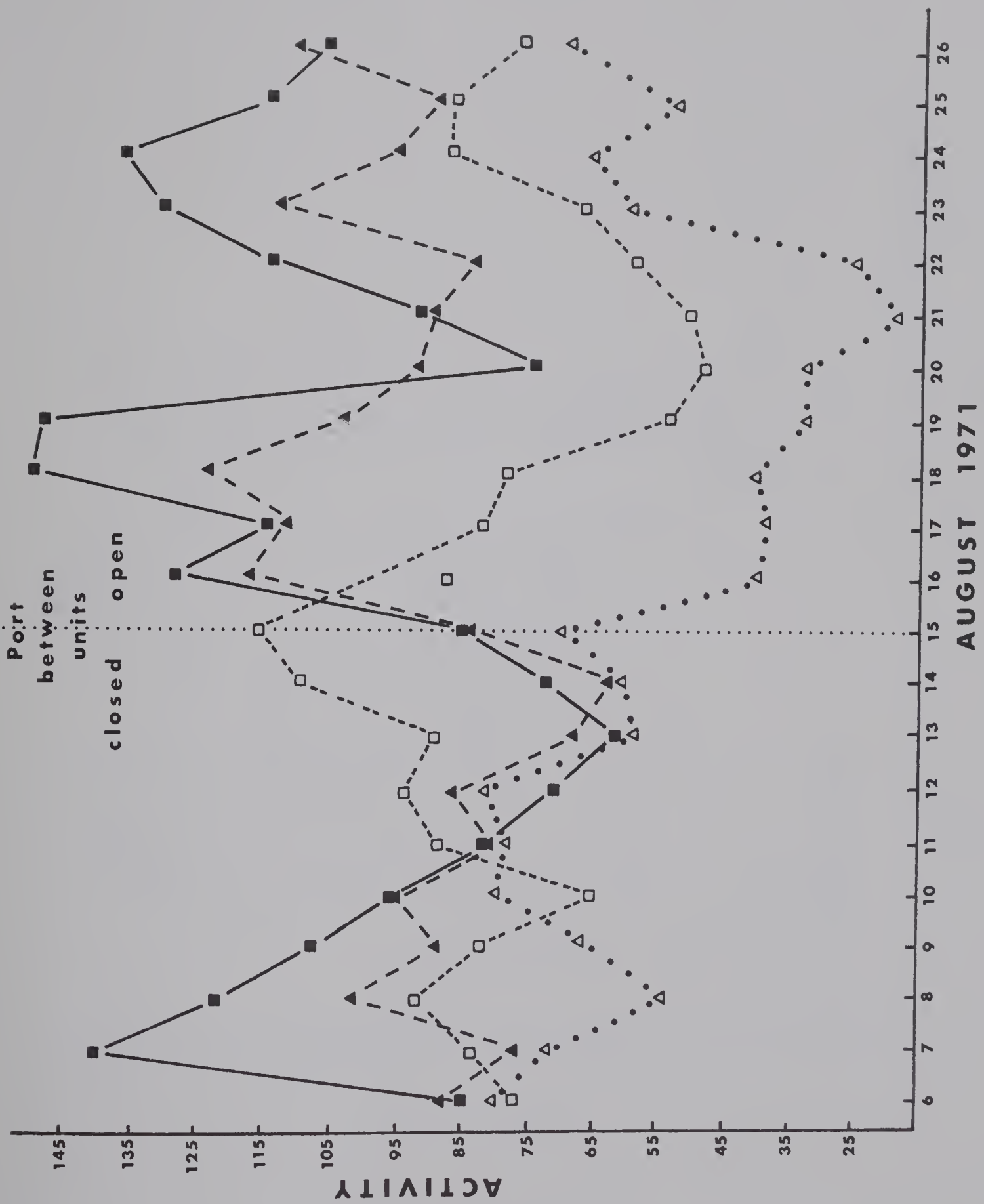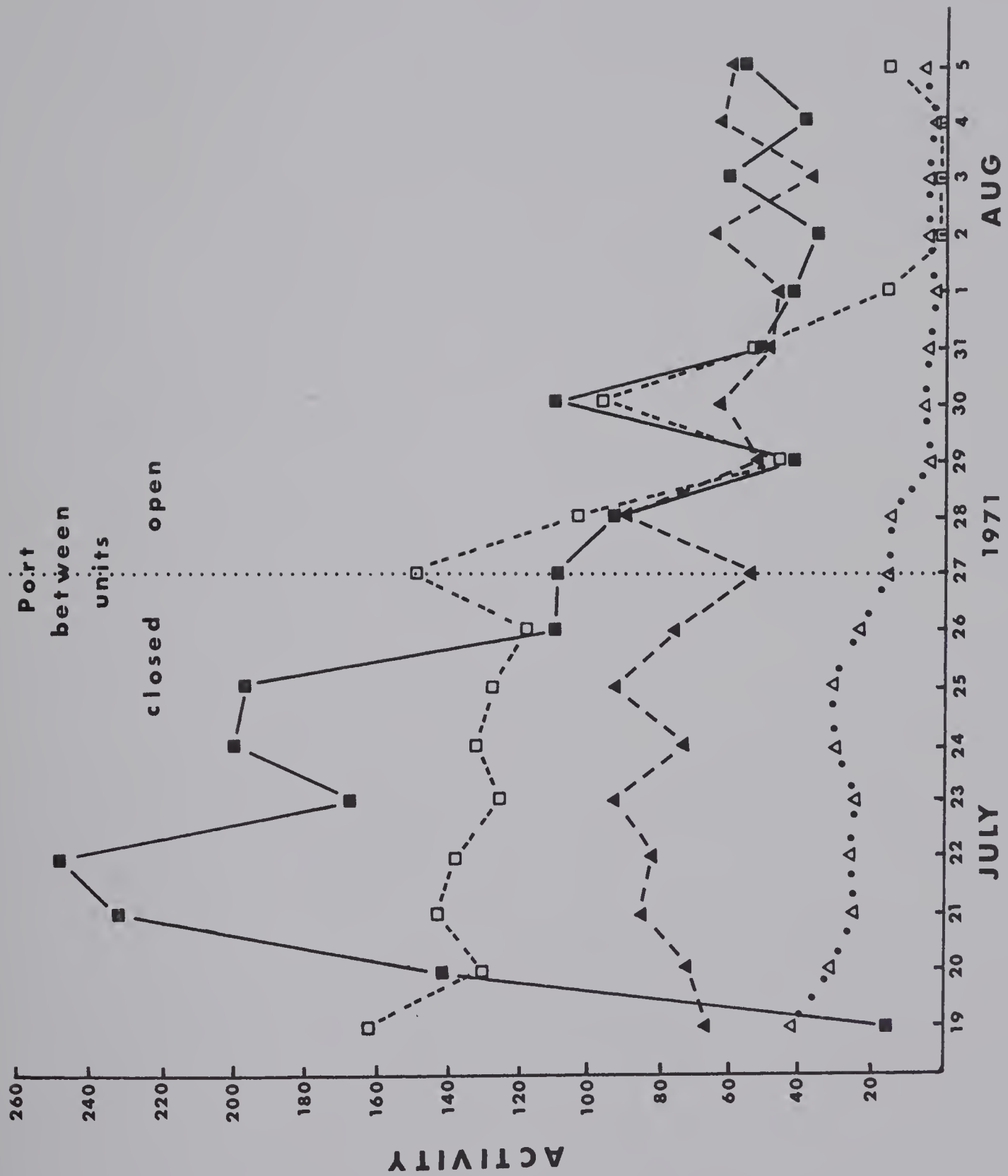
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Figure 30. Example of interactions between *C. gapperi* juveniles and

C. rutilus adults in pens A and D of second Heart Lake

enclosure

       □   Nest boxes in pen A

       △   Feeders in pen A

       ■   Nest boxes in pen D

       ▲   Feeders in pen D

Prior to 27 July only *C. gapperi* were in pen A and only *C.*

rutilus were in pen D. After the port joining units was

opened both species had access to each side. See Fig. 28

for explanation of activity.